

# **Zellen- und Befruchtungslehre** in Einzeldarstellungen

herausgegeben von

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## **Die Geschlechtschromosomen**

von

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# THE SEX CHROMOSOMES

by

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## INTRODUCTION

The present work is an attempt to collect available information on the subject of the sex chromosomes, the viewpoint being in the main that of the cytologist. From the time of SCHLEIP's splendid treatment of sex chromosomes in his general consideration of sex determination ('12) to WILSON's more recent summary ('25a) in his monumental survey of cytology, the status of these chromosomes has been taken up more or less completely in a number of treatises (MORGAN, '13; DONCASTER, '14, '20; BUCHNER, '15; AGAR, '20; SHARP, '21; COWDRY, '24). A survey like the present one can therefore not escape a great deal of repetition, even though no general works like those mentioned can treat the large volume of information on sex chromosomes in an exhaustive manner. It is mainly in this latter respect that a renewed treatment of the subject seems justified.

It has been my aim to emphasize especially those points which still present obstacles to a complete understanding of the nature of sex chromosomes. In the brief treatment of the relation of these chromosomes to the process of sex determination the experimental as well as the cytological evidence had to be considered, a fact which only reflects the interlocking of these two modes of attack in the more recent attempts to solve old problems.

I would like to express my gratitude for the aid given me by my wife, SALLY HUGHES-SCHRADER, in the preparation of the manuscript. To almost as great an extent am I indebted to Dr. A. H. STURTEVANT of the Carnegie Institution whose unselfish help is always so readily given. Dr. C. B. BRIDGES, Dr. C. W. METZ and Dr. C. STERN furnished the originals for the figures 25A and B, 27 and 25C respectively. Finally I am obliged to Professor P. BUCHNER who in his capacity as editor has helped in more ways than one.

## HISTORY

During the final twenty years of the last century various investigators described, figured, and discussed certain structures which in the light of more recent work may have been sex chromosomes. Usually however no definite conclusion on this point is possible and it seems fruitless to consider such investigations as that of LOEWENTHAL ('88) on the cat, LUKJANOW ('89) on *Ascaris mystax*, and SANFELICE ('88) on rodents, with the question of priority in mind. Indeed none of these earlier observers definitely identified such structures as chromosomes.

The first account of what was undoubtedly a sex chromosome was given by HENKING ('91) who described in *Pyrrhocoris apterus* a "peculiar chromatin element" which is condensed in the preparatory phases of the primary spermatocyte. In the first spermatocyte division the twelve elements found in the metaphase plate all divide normally. In the second division one of the twelve elements lags and finally passes undivided into one of the two daughter cells. As a result two types of spermatids are formed, one having 11 and the other 12 elements. After the chromosomes in the spermatids have become diffuse, a "nucleolus" is visible in some of them but not in others (fig. 1). In spite of the clearness of the case HENKING appears to have been hesitant about calling

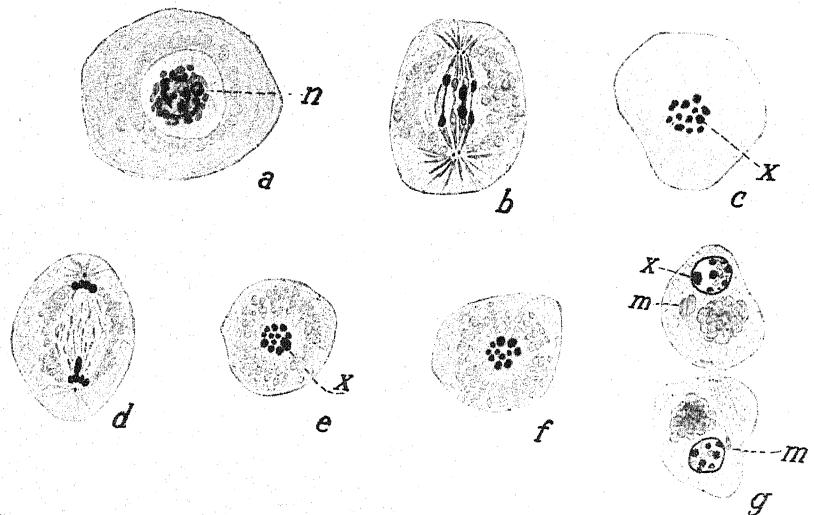


Fig. 1. *Pyrrhocoris apterus* (HENKING, '91)—*a* Growth stage of first spermatocyte (*n* = nucleolus). *b* First spermatocyte division. *c* Daughter plate of first spermatocyte division (*X* chromosome labeled). *d* Late anaphase of second spermatocyte division. *e* & *f* Two daughter plates of second spermatocyte division, one with and the other without the "peculiar chromatin element" (labeled *X*). *g* Spermatids still connected, with one showing the *X* chromosome.

his "peculiar chromatin element" a chromosome. Indeed he calls it a "nucleolus" at times and in his drawings also labels it *X*. But there can be doubt neither of the nature of the element in question nor of the fact that HENKING did not confuse it with a plasmosome or true nucleolus.

In the following decade a number of similar discoveries were made in other forms. WILCOX ('95) observed in the spermatogenesis of *Caloptenus (Melanoplus)* a "nucleolus" which as his description indicates was probably identical with the sex chromosome of that animal. A discovery similarly vague was made by WAGNER ('96 a & b) in spiders. MONTGOMERY's account of a "true nucleolus" in *Pentatomida* published in 1897 was open to the same criticism, but in another report on the same animal in the following year he took cognisance of a "chromatin nucleolus" which

condensed precociously in the growth stages of the primary spermatocyte and was distinct from the true nucleolus. His observations on the behavior of this body in the actual division stages were however not correct, if he was dealing with the sex chromosomes. In the same year, 1898, PAULMIER recorded in *Anasa tristis* conditions very similar to those reported by HENKING in *Pyrrhocoris*. In the second spermatocyte division eleven chromosomes go to one pole and only ten to the other. The odd element he definitely called a chromosome, but confused it with the small m chromosomes in the growth stages. Erroneous counts of the chromosomes seem to have been in part responsible for his failure to correctly follow the sex chromosome through these stages.

In 1899 McCLUNG studying the spermatogenesis of *Xiphidium* made an error that was similar to one previously made by MONTGOMERY in that he apparently believed that the "accessory" chromosome there divides in both spermatocyte divisions. However his description of the behavior of this chromosome in the growth stages is excellent and received confirmation not only in his own work on *Hippiscus* ('00) but also from SUTTON's account of the behavior of the "accessory" in the spermatogonia of *Brachystola* ('00). Miss WALLACE's report of an accessory in spiders published in the same year was rather inconclusive.

In 1901 were published several accounts of the behavior of sex chromosomes. DE SINETY described correctly the behavior of the unpaired sex chromosome (his "Chromosome spécial") in the male of *Orphania* and also gave the first description of a case of a multiple chromosome (a sex chromosome united with an autosome) in *Leptynia*. MONTGOMERY ('01 a & b) showed that in several species of Hemiptera a "chromatin nucleolus" passes undivided to one pole in the second spermatocyte division, thus in a sense correcting his earlier interpretations. But by far the most significant paper in 1901 was one in which McCLUNG reviewed some of the work previously reported on the chromosome under discussion and suggested that the two classes of sperms which must result from the meiotic distribution of the "accessory" are causally related to the production of two sexes. His statement on this point was as follows: "Upon the assumption that there is a qualitative difference between the various chromosomes of the nucleus, it would necessarily follow that there are formed two kinds of spermatozoa which, by fertilization of the egg, would produce individuals qualitatively different. Since the number of each of these varieties of spermatozoa is the same, it would happen that there would be an approximately equal number of these two kinds of offspring. We know that the only quality which separates the members of a species into these two groups is that of sex. I therefore came to the conclusion that the accessory chromosome is the element which determines that the germ cells of the embryo shall continue their development past the slightly modified egg cell into the highly specialized spermatozoon."

Here then, as also slightly later ('02 b) McCLUNG definitely associated the accessory chromosome with sex determination. His main hypothesis was however coupled with the subsidiary one of selective fertilization and led him to the conclusion that the sperm carrying the accessory chromosome is male determining. On this basis it is to be expected that the male carries one chromosome more than the female.

The error was in large part due to the fact that so little was known about the chromosomes in the female.

Mc CLUNG gained confirmatory evidence for his main thesis from his further studies on Locustidae ('02 a) as well as from observations on other Orthoptera by BAUMGARTNER ('02 & '04) and SUTTON ('02). The latter however also confirmed Mc CLUNG's erroneous interpretation in regard to the chromosome numbers in the two sexes by reporting that the spermatogonia of *Brachystola* show one more chromosome than the ovarian follicle cells. Peculiarly enough, Mc CLUNG's general conclusion in regard to the correlation between the accessory and sex determination received very little additional support for the first few years. Several investigators concluded that the accessory originates from the union of two small spermatogonial chromosomes (as for instance Mc GILL, '04; VOINOV, '04; MONTGOMERY, '04, '05; ZWEIGER, '06). This difference of opinion rested partly on the fact that these investigators were dealing with the incompletely understood XY condition, and also as in the case of ZWEIGER on special, complicating conditions in the species studied.

One of the most persistent opponents to the hypothesis advanced by Mc CLUNG was GROSS, who endeavored to show that in both *Syromastes* ('04 a & b) and *Pyrrhocoris* ('06) the accessory as found in the spermatocytes arises from two small spermatogonial chromosomes and also that the number of chromosomes is the same for both sexes. It was his opinion as well as that of Miss WALLACE ('05) that all sperms lacking the accessory degenerate and that therefore there is only one type of sperm that can fertilize the egg. It is clear that this view if correct, would cause Mc CLUNG's hypothesis to fall to the ground.

The confusion was cleared up in a most striking manner by the work of Miss STEVENS ('05) and WILSON ('05 a & b), whose publications appeared almost simultaneously. STEVENS working on *Tenebrio* and WILSON on several *Hemiptera*, discovered that in the males of these forms there is one unequal pair of chromosomes and that this pair behaves in the growth stages of the spermatocytes like the odd or unpaired element which Mc CLUNG had called accessory. They found further that the members of this unequal pair separate and pass to opposite poles in one of the two meiotic divisions. STEVENS also demonstrated that in the female the diploid number of chromosomes is the same as that of the male but that no unequal pair is present. Both observers realized fully the significance of their findings and as a consequence the error that had been involved in Mc CLUNG's assumption that males carrying an accessory have one more chromosome than the females was soon corrected.

Other confusions and misunderstandings were cleared up especially by WILSON, who in a series of brilliant papers analyzed the various modifications of sex chromosomes in the heterogametic sex and showed how the basic conditions represented by an unequal pair of sex chromosomes may be related to these obtaining in cases where the X chromosome has no partner, and how modifications may arise due to the presence of compound chromosomes, supernumeraries, and m chromosomes.

Although these conclusions were now very quickly accepted by most of the workers in the field, there nevertheless existed some opposition and resultant controversy. The objections voiced by GROSS were

disposed of by WILSON ('09 a & c) in showing that the male of *Pyrrhocoris* has an unpaired sex chromosome in the spermatocytes and that this arises from a single spermatogonial chromosome of corresponding size and not a pair of smaller spermatogonial chromosomes. The chromosomes of the female supported this conclusion. In *Syromastes* WILSON showed that GROSS had indeed observed correctly that the male has two sex chromosomes, but he also demonstrated that these two chromosomes represented the components of a compound X chromosome which is unpaired. Again the chromosomes of the female bore out this conclusion for there each of the two components is represented twice and the diploid number is therefore greater by two chromosomes than that of the male. A more general controversy arose from the claims of FOOT and STROBELL ('07 a & b) that in *Anasa tristis* the spermatogonial number of chromosomes is 22 as in the female, and that there is neither an odd chromosome or an unequal pair of chromosomes in the male. Advanced by two such careful workers, these findings were received with a good deal of attention, but there now seems to be no doubt that they were actually in error and that the male has 21 and not 22 chromosomes.

Further investigation served only to establish more firmly the general conclusions regarding the correlation of sex chromosomes to sex determination. On the other hand, the great simplicity and clearness of the sex chromosome theory in its general aspects was perhaps accountable at times for rash conclusions and possibly also for a tendency to regard with suspicion those cases which did not seem to conform to the simplest conception of the theory. It was in this connection that investigations like those of VON BAEHR and MORGAN on the life cycles Aphids and *Phylloxera* had a good influence, for there was demonstrated with great clearness that even very complicated and apparently confused conditions may rest on a basis very much like that observed in the simplest cases.

It is perhaps unnecessary to say that we have not reached the final conclusion on the relation between sex chromosomes and sex determination. The final analysis of what the correlation really rests on is not possible through investigations embodying only pure cytology. Realization of this fact has already brought into the field the experimental attack as represented by the geneticist, and the gratifying results incorporated in such work as that of STURTEVANT ('21) and BRIDGES ('22) show that this new direction is the right one.

## NOMENCLATURE

The somewhat bewildering terminology that has come into use as our knowledge of the sex chromosomes increased, is in part a reflection of the history of investigations in this field. Even today there are no generally accepted terms, and the designation "sex chromosome" is generally used in the present treatise simply because it seems most obvious and natural.

The terms which cover sex chromosomes of any kind may be listed as follows:

Chromatin nucleolus	MONTGOMERY, 1898
Chromosome spécial	DE SINETY, 1901
Modified chromosome	MONTGOMERY, 1901
Heterochromosome	" , 1904
Allosome	" , 1906
Idiochromosome	WILSON, 1905
Heterotropic chromosome	" , 1906
Sex chromosome	" , 1906
Differential chromosome	" , 1906
Eccentric chromosome	FOOT & STROBELL, 1907

It is to be understood that several of the above terms may be used to designate other chromosomes as well as sex chromosomes. This is especially true of heterochromosome and allosome, both of which have been used repeatedly with the understanding that their use is confined to the sex chromosomes proper, whereas MONTGOMERY stated emphatically that he intended these terms for any kind of chromosome distinguishable from the ordinary autosomes by certain peculiarities of behavior. It is plain that on the basis of such a definition such chromosomes as supernumeraries, heteromorphic chromosomes and m chromosomes would be included as well as sex chromosomes. A similar objection might be made to the use of "eccentric chromosome" as applied to sex chromosomes exclusively, since FOOT and STROBELL were of the opinion that the chromosome to which they applied this name has nothing to do with sex determination.

A number of more specific terms has come into use to designate the nature of any single sex chromosome in question. The necessity for this arose from the fact that in some cases the sex chromosome in the heterogametic sex has no partner, whereas in other cases this sex has two unequal sex chromosomes.

Accessory chromosome	MC CLUNG, 1899
Odd chromosome	MONTGOMERY, 1901
Chromosome X	" , 1901
Monosome	" , 1906
X chromosome	WILSON, 1909
Y chromosome	" , 1909.

Here the term X chromosome to designate the sex chromosome which is represented twice in the homogametic sex and only once in the heterogametic sex is perhaps the most widely used, although all the others are still employed. Under Y chromosome is meant the chromosome which as the partner of the X is found only in the heterogametic sex.

To avoid confusion in those cases (birds and Lepidoptera) in which the female is heterogametic instead of the male as in all other known forms, MORGAN has suggested that the letter Z be used for the sex chromosome present twice in the homogametic sex (i. e. in this case the male) while W be used for the sex chromosome found only in the heterogametic sex.

There remain some terms used in connection with complications in which the sex chromosomes may play a part. In certain cases the X—and much more rarely the Y—may be represented by several separate elements. The origin of such sex chromosomes need not be discussed here. The terminology however is confusing. Thus DON-

CASTER ('20) used the term "multiple X", but Mc CLUNG had used the term "multiple" in 1917 and earlier to cover cases in which two or more chromosomes become attached to each other (thus a union of two autosomes belonging to different pairs, or union of a sex chromosome with an autosome). Again the same term has been applied more recently in those forms in which the number of chromosomes has been increased to a multiple of a supposed basic number (as in the roses). Finally, WILSON ('25 a) has used the term "compound chromosome" for cases in which a chromosome is represented by several components. To this also may be made the objection of ambiguity for strictly speaking the meaning of this word also covers cases in which an apparently single chromosome is composed in reality of two or more whole chromosomes that have undergone fusion. As matter of fact, DONCASTER ('20) actually used the term in this latter sense.

But rather than add new terms to an array already so bewildering, I propose to use here the following:

Compound sex chromosome — to designate those cases in which the X or Y are represented by two or more components.

Multiple chromosome — to designate chromosomal formations brought about by the adherence or union of two or more non-homologous chromosomes to each other, with no implication of a meiotic process<sup>1</sup>.

## GENERAL MORPHOLOGY AND BEHAVIOR

In all cases where a cytological demonstration of sex chromosomes is possible, their part in the chromosome cycle is a relatively simple matter—as long as we are concerned only with the more general aspects.

In one sex, the full or diploid set of chromosomes is composed of two equal haploid sets. Thus although the members of the haploid set may show the widest variation in size and form, each chromosome has one homologous partner in the other haploid set. In the course of meiosis these partners are separated from each other and the gamete when ready for fertilization carries only one complete haploid set. It is evident that individuals of this kind can produce only one type of gamete, that is, they are said to be homogametic.

An examination of the diploid set of chromosomes in the opposite sex presents one basic difference. This may express itself in one of two basic ways, each one of which is subject to certain complications. In one case the diploid number is one less than that of the homogametic sex, so that consequently one of the chromosomes has no partner. This odd or unpaired chromosome is the sex chromosome which is usually designated as X. The gametes produced in this sex are of two types, differing in the fact that half of them carry an X and half do not.

If size or form distinguish the X, an analysis of the chromosomes in the homogametic sex will show that it is there represented twice. The sex chromosome conditions can therefore be briefly indicated as follows: Homogametic = XX; Heterogametic = XO. Except in the cases of

<sup>1</sup> But recently the term has also been used as an equivalent of the German term "Sammelchromosom" as applied in cases like the bee. Strictly speaking, this is not justifiable, since we know practically nothing about the nature of the chromosomes that there become joined at certain stages.

the birds and Lepidoptera<sup>1</sup>, it is the female sex that is homogametic, so that with these exceptions in mind the chromosome cycles may be represented schematically as follows, (A = haploid set of autosomes):

$$\begin{aligned}\text{Egg (A + X) + Sperm (A + O)} &= 2A + XO = \text{Male} \\ \text{Egg (A + X) + Sperm (A + X)} &= 2A + XX = \text{Female.}\end{aligned}$$

In the alternative case, the X in the heterogametic sex has a partner. This however is not its homologue, differing in size or form and undergoing no synapsis with it. It is usually designated as Y. In the meiotic process two types of gametes are again formed, one carrying in addition to the autosomes an X, and the other a Y. Heterogamety is therefore expressed here as XY and the cycle is:

$$\begin{aligned}\text{Egg (A + X) + Sperm (A + Y)} &= 2A + XY = \text{Male} \\ \text{Egg (A + X) + Sperm (A + X)} &= 2A + XX = \text{Female.}\end{aligned}$$

Sex chromosomes have been cytologically demonstrated in many forms of Platyhelminthes, Nematelminthes, Echinodermata, Arthropoda, Mollusca, Vertebrata and a few plants. However, in many other forms in these phyla sex chromosomes have never been seen nor has a conclusive cytological demonstration of their presence been made in the Porifera, Coelenterata, Nemertinea, Trochelminthes, Protochordata, and Molluscoidea.

In the heterogametic sex the sex chromosomes are usually recognizable on the score of special behavior as compared with the autosomes. This behavior most often takes the form of heteropycnotosis, that is, the sex chromosomes undergo precocious condensation in the growth stages. This tendency is not merely the outward expression of the fact that changes occur more rapidly in the sex chromosomes, for there is often the additional tendency to remain condensed longer than the autosomes after the completion of the division, and in some cases the sex chromosomes never become as diffuse as the autosomes during meiosis. In addition to heteropycnotosis the sex chromosomes may be distinguishable because of precession or lagging (succession) on the spindle; they may take a special position with respect to the autosomes; they may lie in a special vesicle during certain of the stages; and they may tend to remain condensed after each meiotic division.

#### MEIOTIC GROWTH STAGES

It is of interest to observe that this special behavior of the sex chromosomes is apparently not manifested prior to the spermatogonial stages. Thus MOHR's careful investigations ('15, '16) on certain forms of the Locustidae led him to conclude that in the somatic cells the unpaired X and the autosomes can not be differentiated on the basis of behavior. However it must not be forgotten that researches touching on the sex chromosomes in somatic cells are small in number and generalization is not justified.

Indeed, certain evidence seems to show that the differential behavior does not always appear suddenly to its most marked extent, that

<sup>1</sup> Genetic evidence (BELLAMY, '23, and GORDON, '26) seems to show that in the fish Platypoecilus it is also the female that is heterogametic.

is to say with the appearance of one definite germ cell generation like the first spermatogonia or the primary spermatocytes. Thus BRUNELLI's work on *Tryxalis* ('10, '11) shows that in the spermatogenesis in which the X is distinguishable from the autosomes in the earliest spermatogonia because of its inclusion in a special vesicle, it is at first subject to the same degree of diffusion. But gradually and with successive generations of spermatogonial cells it evinces an increasing tendency to precocious condensation and this progressive heteropycnosis becomes most pronounced in the spermatocyte growth stages. On the other hand cases are known in which heteropycnosis does not occur even in the last spermatogonial generations of cells but appears to a striking degree in the primary spermatocytes (*Oncopeltus*, WILSON, '12). Again it is manifestly not possible to generalize.

The formation of chromosome vesicles is not confined to sex chromosomes. However, even when there are autosomal vesicles, the vesicle of the sex chromosomes maintains a certain degree of distinctness which is due in great part to the fact that it does not share the tendency to fusion with other vesicles such as is evinced by those of the autosomes. But even in the single order of Orthoptera where vesicle formation is very marked, a great deal of variation has been observed. Thus WENRICH ('16) has observed in *Phrynotettix* vesicle formation of the sex chromosome in several generations of spermatogonial cells but not the last, while DAVIS ('08) specifically mentions that in some other forms it is present in its clearest form at that stage. But it is safe to state that vesicle formation is not confined to the meiotic period but is sometimes to be encountered in various spermatogonial stages as well.

If there is thus a great deal of variation in regard to the stage at which the sex chromosomes first show a distinctive behavior, the way in which this distinction is expressed is subject to a bewildering amount of variety. This is especially true during the meiotic period. As far as the preparatory phases for this period are concerned a sharp contrast is presented in a comparison of even such closely related groups as two orders of insects like the Hemiptera and Orthoptera. In most Hemiptera these preparatory changes seem relatively simple. After the last spermatogonial telophase the autosomes and sex chromosomes become diffuse so that the nucleus at this time presents a typical resting condition. With the transition to the prochromosome stage the sex chromosomes attain a differential aspect in that they are smoother in outline, more compact, and stain more intensely with chromatin stains. This stage is succeeded by one in which the autosomal prochromosomes give rise to delicate, much coiled threads but to all appearance the sex chromosomes do not take part in this process and remain compact just as they do during all the succeeding changes (leptotene, synaptotene, pachytene, diplotene, confused, and diakinesis stages) that are observable in the autosomes. In some forms a nucleolus makes its appearance at some stage during these preparatory steps, but its exact relation to the sex chromosomes is not clear. Again, some variability is encountered in the compactness assumed by the sex chromosomes; thus *Lygaeus* has the X and Y elongated during a time when the sex chromosomes of *Oncopeltus* are quite lumpy and compact (fig. 2). Finally a considerable diversity is shown in regard to the time at which the

equational split first appears in the sex chromosomes, and while such a division line is visible already in the diplotene phase of *Lygaeus*, it does not appear in the sex chromosomes of *Oncopeltus* until after the confused period.

The apparent lack of activity of the sex chromosomes at a time when the most far reaching changes occur in the autosomes has led

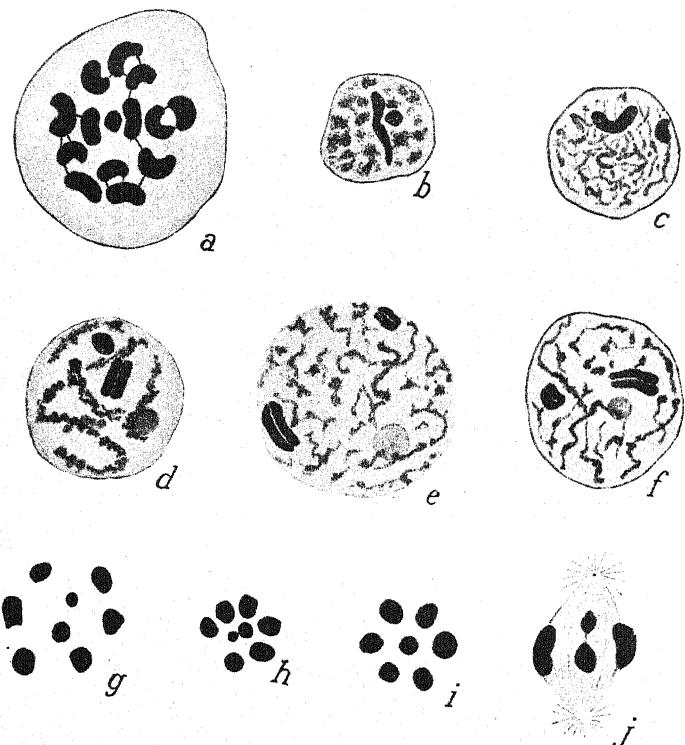


Fig. 2. *Lygaeus biceruris* (WILSON, '12)—*a* Spermatogonial metaphase. *b* Spermatogonial telophase showing X and Y in condensed state. *c* Leptotene stage of first spermatocyte with X and Y condensed. *d* Diplotene stage of first spermatocyte with X and Y condensed, and a nucleolus showing. *e* Confused stage of first spermatocyte. *f* Prophase stage of first spermatocyte. *g* Metaphase of first spermatocyte division, with X and Y in middle of plate. *h* Daughter plates of first spermatocyte division. *i* Metaphase of second spermatocyte, with X and Y joined in middle of plate. *j* Second spermatocyte division showing X and Y going to opposite poles.

various observers to the conclusion that we are concerned with degenerating structures that are on the way to disappearance (PAULMIER, '99, MONTGOMERY, '05). But GUTHHERZ ('22) reaches a conclusion almost directly opposed, for in assigning to sex chromosomes a special position among chromosomes he points out that his observations of their secretion of much nucleolar material as well as the distinct space that nearly always separates them from the autosomes bespeak a greater chemical activity rather than a less.

In view of this question of their nature and activity, it is of some importance to observe that in some forms, notably the Orthoptera, the sex chromosomes do not appear as semi-dormant structures but undergo changes that parallel closely those observable in the autosomes. These facts have been brought out especially in the various accounts published by MC CLUNG and his students as well as by MOHR and some other workers.

As has already been remarked, the sex chromosomes in the males of most Orthoptera are recognizable already in the spermatogonia — whether because of heteropycnotosis, inclusion in a special vesicle, or both (fig. 3 and 18). In the meiotic preparatory stages the X generally does not elongate as much as the autosomal threads, although in some species like *Xiphidium* it may attain the form of a coiled spireme thread differing only slightly in diffusion and length from those of the autosomes. At the time of the bouquet stage when the ends of the autosomal threads become polarized and synapsis occurs, the ends of the X are also drawn to the same point — and this occurs even in those cases in which the X chromosome's thread is relatively short and condensed. The "conflexion of the heterochromosome" as this phase is termed by MOHR is quite evidently identical with the similar phase described in the autosomes. The point of the X at which the bend has occurred in the conflexion then swells and becomes vacuolated, but as long as the autosomes remain polarized no other change is noticeable. It is only when the diplotene or split stage is reached and the polarized ends of the autosomes once more become free that a similar liberation of the X occurs. Its outline then again becomes smooth and it once more becomes compact. At the same time appears the equational split, quite equivalent to the split that makes its appearance simultaneously in the autosomes. As WENRICH ('16) has well stated in his consideration of the sex chromosome, "its behavior, while unique in many respects, differs from that of the autosomes in the degree and the chronology, rather than in the kind of its changes" (fig. 4).

The question of pairing of course does not arise in those cases in which the X is an odd element and has no partner. When a Y is present however, the behavior of the two sex chromosomes with respect to each other is of some interest. In many Hemiptera the X and Y remain separated throughout the preparatory phases and show absolutely no relationship to each other in their position in the nucleus. In other cases they are united in the growth stages but separated in the dia-kinesis. This separation is maintained in the equational division, but prior to the division in which they pass to opposite poles they may come together for a moment only to separate almost immediately in the following division. Finally in still other cases, like some Coleoptera, the X and Y may be united to form a single chromosome nucleolus that maintains its form up to the time of the maturation division. In none of these types is the nature of the pairing quite clear.

#### MEIOTIC DIVISIONS

The relation of the sex chromosomes to the autosomes in their position in the metaphase plates of the two maturation divisions is again quite variable. In some Hemiptera, their position in the first metaphase

seems to be fairly constant (always in the center as in *Lygaeus* (fig. 2), or slightly at one side of the group of autosomal tetrads as in *Syromastes*), but in most other forms no such regularity obtains.

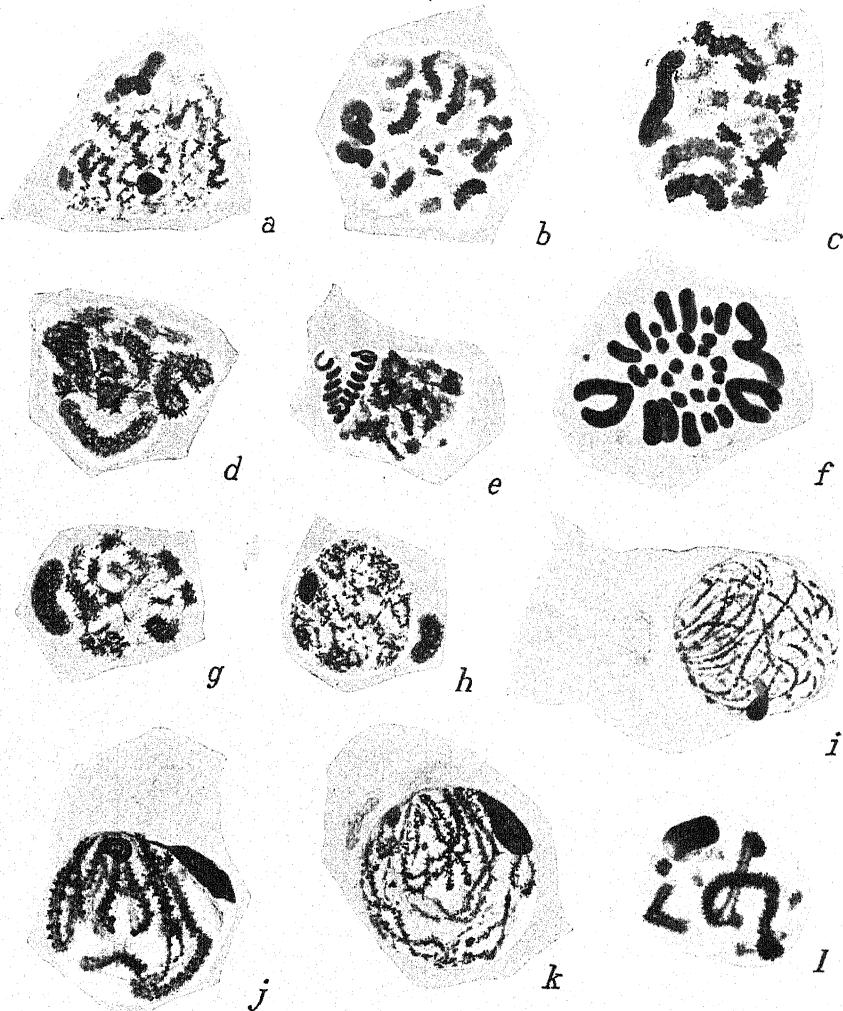


Fig. 3. *Locusta viridissima* (MOHR, '16)—a, b & c Prophase stages of primary spermatogonia. d, e & f Prophase stages of secondary spermatogonia. g & h Steps in formation of leptotene threads of first spermatocyte, showing the X at one side in the cytoplasm. i Leptotene stage. j Pachytene stage. k Diplotene stage. l Prophase.

Whether the sex chromosomes pass undivided to the poles in the first (preheterokinesis) or the second spermatocyte division (postheterokinesis), their behavior in whatever division is reductional for them often brings out another feature which has at times been regarded as diagnostic of sex chromosomes. That feature lies in the fact that the sex chromo-

somes in some forms precede the autosomes to the poles or as in others lag behind them on the spindle. But whether we are dealing with precession or succession (lagging), it is now clear that these characteristics are not absolutely confined to sex chromosomes, even though much more commonly met with there than in other chromosomes. The behavior is usually constant in its character for any one species but even very

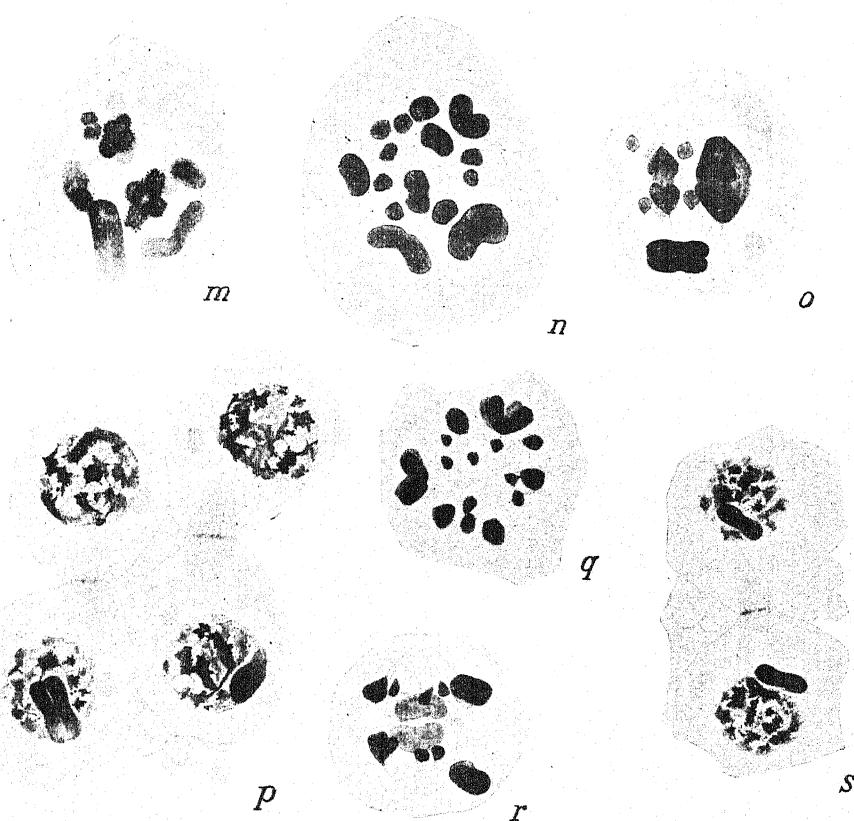


Fig. 3. *m* Late prophase. *n* Metaphase of first spermatocyte. *o* Anaphase of first spermatocyte. *p* Interkinesis. *q* Metaphase of second spermatocyte. *r* Anaphase of second spermatocyte. *s* Spermatids.

closely related species may differ decidedly in this respect from each other. Indeed in some exceptional cases like that of *Vanduzea* (BORING, '07) either precession or succession may occur in different primary spermatocyte cells of the same testis.

The actual divisions occur as might be expected. In one of the meiotic divisions, the sex chromosomes are divided equationally, and in such a division the split which usually appears already in the growth stages, is consummated. In the other division however, the sex chromosomes pass undivided to the poles—in case of an XY pair always to opposite poles.

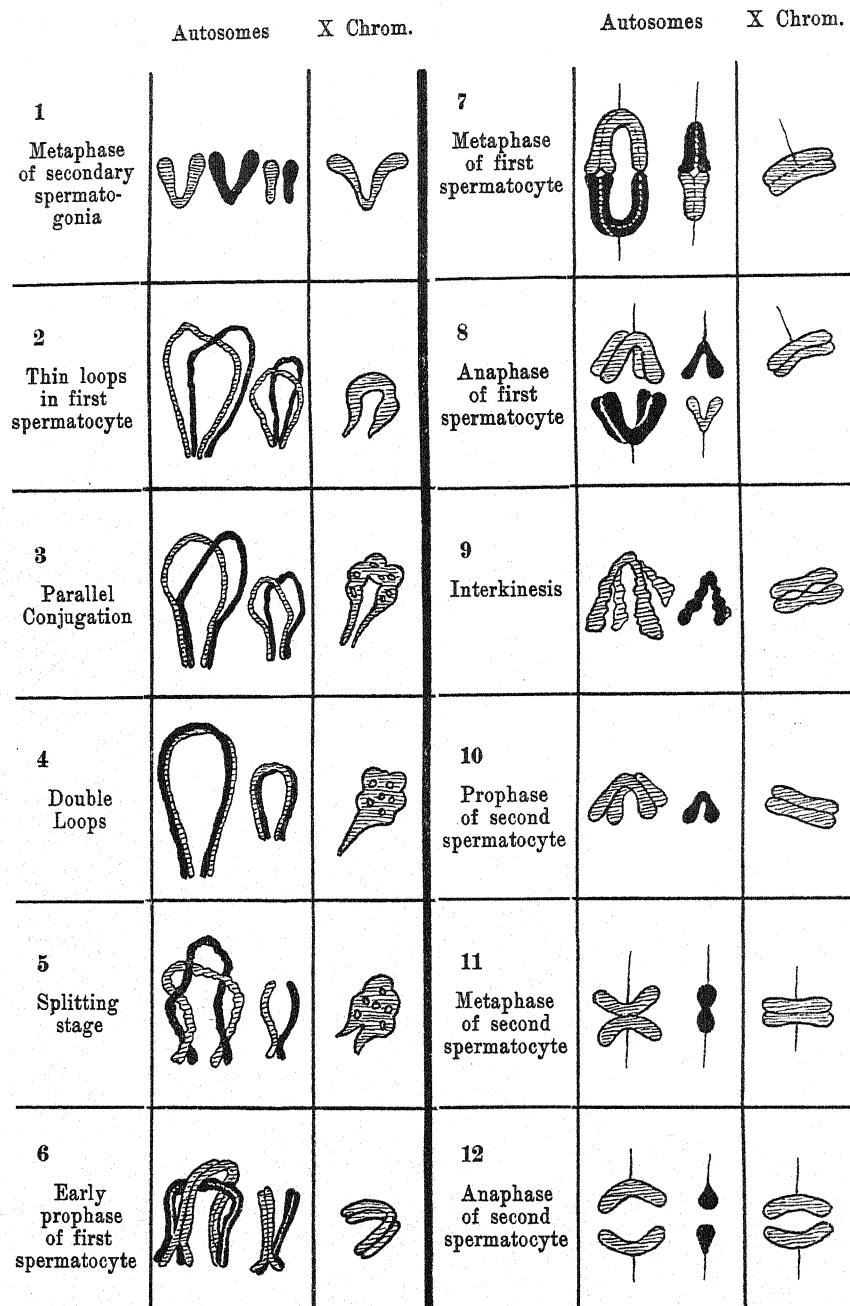


Fig. 4. MOHR, ('16)—Diagram showing the behavior of the X chromosome in *Locusta*.

Between the two maturation divisions occurs the interkinesis during which the autosomes generally become more or less diffuse. Here again the sex chromosomes betray their tendency to remain condensed and usually do not reach the grade of diffusion attained by the autosomes.

### SEX CHROMOSOMES IN THE GAMETES

The preceding observations with regard to the interkinesis apply more or less to the stages following the second maturation division. Thus the sex chromosomes may often be recognizable in the network formed by the diffusing autosomes simply because they remain compact for a long time. But once more, no generalization is possible, for the spermatids of a great many forms show no trace of such persistence even though sex chromosomes are definitely known to be present. On the other hand the presence of true nucleoli during the early stages of spermatid formation may often lead to confusion and thus the body seen in all spermatids of *Ceresa* (BORING, '07) is a true nucleolus, whereas the same observer reports that a similar body in *Campylenchia*, a closely related form, represents the sex chromosome.

With very few exceptions (as in *Ancyraanthus*, MULSOW, '12) the presence of sex chromosomes in the completely formed gametes can not be established. However, it might be expected that in cases where the Y if present is quite small and the X very large, the heads of the completely formed sperms would show size differences correlated with the amount of chromatin represented by the sex chromosome. In rare cases this expectation seems actually to be realized, but in most instances the difficulty of making accurate measurements as well as additional complicating factors have prevented a final conclusion.

Although the general behavior of the sex chromosomes thus seems well established, a great deal remains to be done in the analysis of processes and structure underlying these more superficial phenomena. It is the purpose of the following pages to review our knowledge of these deeper lying factors.

### CONFUSING ELEMENTS

It may safely be stated that it is impossible to isolate any one feature of behavior and regard it as diagnostic of sex chromosomes. The confusion that has often arisen in the study of sex chromosomes is attributable in large part to the more or less arbitrary assumption that one or a few reactions are specific for them, and this despite the fact that several of the earlier workers like WILSON were aware of this danger and warned against it. The last decade has brought on a more cautious attitude however, and in several groups like the mammals where much superficial work characterized earlier investigations, a realization of the difficulties attending the recognition of sex chromosomes is gradually bringing order out of chaos.

A detailed consideration of the sources of confusion would partake too much of a digression, and since a thorough review of the elements involved has been given in such treatises as that of WILSON ('25a),

only a brief summary will be given here. In such a summary the confusing elements may be given as follows:

True nucleolus or plasmosome.—In typical cases this intranuclear body is oxyphilic and stains with acidic dyes. If therefore a cell is stained with a combination of basic and acidic dyes, the chromatin elements usually stain with the former and the nucleolus with the latter. However there are exceptions to this, and in cells stained with FLEMMING's triple stain the nucleoli may stain with safranin, which as a basic stain also colors the chromosomes. Again, just like the chromatin, the nucleoli may vary in their staining reactions with the various phases of the nucleus. Finally the mode of fixation may definitely affect this staining reaction. In view of this uncertainty a final identification of the nucleolus and its differentiation from sex chromosomes must rest on a study of the complete cycle of the various changes in the cell elements.

Chromatin nucleolus or karyosome.—The term chromatin nucleolus was used by MONTGOMERY in 1898 as a designation for the sex chromosome. But it is now quite clear that nucleolus-like bodies which typically take a basic stain are not always identical with sex chromosomes. Thus lumps and knots of a chromatinic nature are frequently encountered in the nuclear network and although these may in some cases furnish material for the sex chromosomes in the later preparatory stages, it is likewise true that in other instances they may also contribute to the formation of the autosomes. Such "netknots" are perhaps closely related to the chromosome nucleoli, which are known to give rise directly to one or more entire chromosomes, and these in turn may have a similar relation to the karyospheres. The latter, of which a nucleus seldom contains more than one or two, may contain all or nearly all of the chromosome material during certain stages of the nuclear cycle—as has been shown for instance in several Myriapoda (fig. 17A) (BLACKMAN, '03 ff.), Hemiptera (BROWNE, '10 ff.) and Coleoptera (HAYDEN, '25). Summing up therefore, it may be said that a chromatin nucleolus may be identical with one or more sex chromosomes, but that autosomes also arise from such structures in some instances.

Amphinucleolus.—These are the bodies of a double nature which partake of the characters of both a true nucleolus and a chromatin nucleolus. In those cases where a chromatin nucleolus is obviously attached to a plasmosome, the combination involved is not confusing. More difficult are those cases in which one or more chromatin nucleoli are actually imbedded in a larger plasmosome. It is almost impossible to differentiate between some instances of this kind and those karyospheres which include a certain amount of plasmosomic material as well as chromatin.

Chromatoid body.—This term has been applied by several observers to bodies as to whose exact nature we are still in doubt. It stains intensely with basic dyes, but with AUERBACH's rubin-methyl green and ALTMANN's stains takes the same color as the mitochondria. But according to PLOUGH ('17) it is not stained by Janus green intra vitam and thus lacks a staining reaction which more than any other is indicative of a mitochondrial nature. However it is to be noticed that as long as the nuclear wall is intact, no confusion with the normal sex

chromosome is apt to arise since the chromatoid body typically lies outside of the nucleus. It is therefore only during the actual division that the chromatoid body is to be found among the chromosomes (fig. 20c) and then may indeed closely resemble a sex chromosome (as for instance in *Pentatoma senilis*). But WILSON ('13) has shown that even in such a case a close study of its behavior will serve to differentiate it from the chromosomes, for with the formation of the new nuclear membrane it is again left in the cytoplasm (fig. 5).

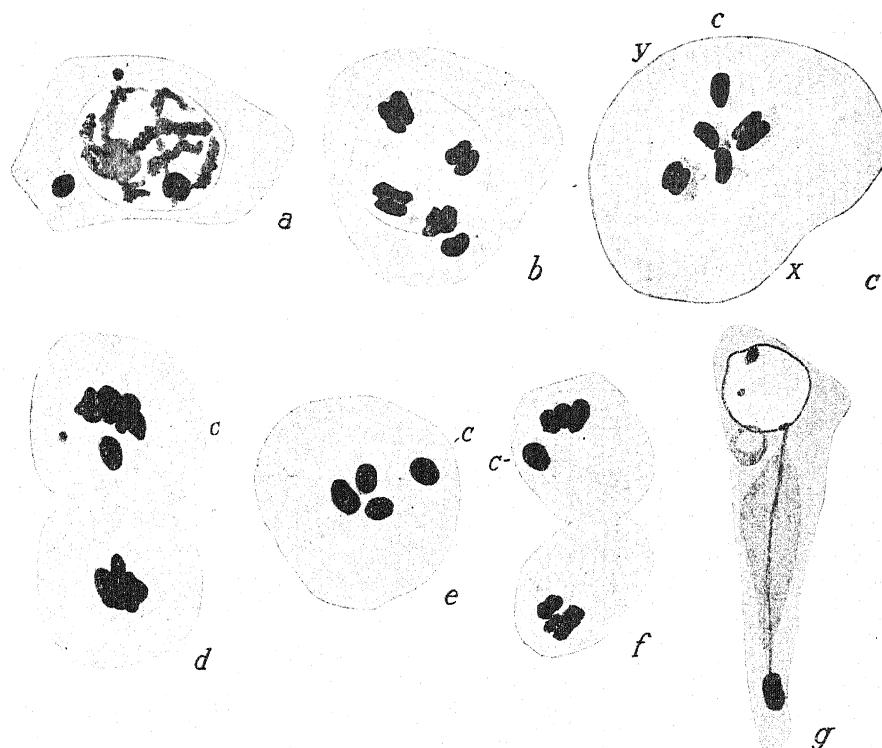


Fig. 5. *Pentatoma senilis* (WILSON, '13')—*a* Early growth period of first spermatocyte, showing chromatoid body outside of nucleus. *b* Late prophase. *c* Metaphase of first spermatocyte division, (*c* = chromatoid body). *d* Late anaphase of first spermatocyte division, with chromatoid body lagging on the spindle. *e* Metaphase of second spermatocyte (*c* = chromatoid body). *f* Late anaphase of second spermatocyte division. *g* Spermatid with chromatoid body below (*a* = acrosome).

Other chromosomes.—Other chromosomes which may be and actually have been mistaken for sex chromosomes are heteromorphic autosomes, supernumeraries and m chromosomes. Thus the unequal size of a heteromorphic pair of autosomes may lead to the conclusion that an XY pair is under observation. Supernumeraries which according to WILSON may have been derived from sex chromosomes may also lead to confusion, and the errors made by several early observers regarding the relation of m chromosomes to sex chromosomes demonstrate sufficiently that they

are not always easily differentiated from each other. Also to be considered are the multiple chromosomes in which a sex chromosome may be joined to an autosome, and in which a correct interpretation may not always be easy.

If on the basis of these considerations, it must be clear that our known staining reactions can not always enable us to identify sex chromosomes, it must not be forgotten that these stains have their distinct value as checks on the conclusions arrived at from a study of the behavior of any element under consideration. Without following such an element through the whole cycle—from resting stage through the various phases of division and back to resting stage—no final conclusion regarding its nature seems warranted. For the further step of differentiating an X from a Y, a still more elaborate study seems to be necessary. PAINTER ('24b) has enumerated five considerations which in his opinion should guide the process of identification of X or Y chromosomes. They may be briefly given as follows (PAINTER assumes that the male is heterogametic):

1. A study of the diploid chromosome complex of the male. If the number is odd, the XO condition is indicated (except in case of some compound X chromosomes or an extra chromosome), whereas an even number would indicate an XY pair (with the exceptions already noted).
2. A study of the haploid complex in the male. If the number is just half the diploid, the XY condition is again indicated (except in case of the compound X of the  $X^I X^{II}$ —O type).
3. A study of the morphology and behavior during meiosis. It is here that the XY conditions are perhaps most easily recognized in most cases.
4. A study of the sex chromosomes that enter the spermatids.
5. A study of the chromosomes in the female.

The importance of knowing the chromosome conditions thoroughly in both sexes can hardly be sufficiently emphasized. It is astonishing how many conclusions in regard to sex chromosomes have been based on a study of the male alone. It is true that the cytological conditions in the female are not always as favorable as those of the male, but many investigators never seem to consider that only a study of the female will serve as a final check on their findings in the male.

The cumbersome set of rules and cautions which is embodied in such outlines of direction as those of PAINTER and others only serves to express the fact that a study of the sex chromosomes is in most cases not a simple proceeding. A study of the whole cell cycle including meiosis in both sexes is the only safe course to follow, and such a study must be conducted with a complete knowledge of the sources of possible confusion.

## HETEROPYCNOSIS OF THE SEX CHROMOSOMES

Perhaps the most striking characteristic in the behavior of the sex chromosomes is their heteropycnosis in the heterogametic sex, especially during the meiotic stages. As has already been pointed out, in some cases and notably in the Orthoptera this behavior does not differ from

that of the autosomes so much in the kind of processes involved as in the degree and chronology of the changes (WENRICH, '16) (fig. 4). In other cases, and here may be mentioned many Hemiptera, this basic similarity in the behavior of sex chromosomes and autosomes is not so evident, but it seems very likely that the cytological conditions are there simply less favorable for detailed observations on this phase.

The reasons that underlie this peculiar phenomenon of heteropycnotosis have never been satisfactorily determined. The realization that with a final elucidation of this problem considerable progress would be made into the analysis of the physiology of chromosomes has however given rise to a good deal of work on this particular aspect.

An hypothesis voiced repeatedly is that all sex chromosomes are undergoing degenerative processes, or as several earlier observers had it, are not chromosomes at all. Both views have met with a great deal of opposition. Thus MOHR ('15, '16) after a detailed and exacting analysis of the behavior of the unpaired sex chromosome in the males of *Leptophyes* and *Locusta* definitely rejected this hypothesis. Like several investigators before him, MOHR emphasized that in the female of those species the sex chromosomes behave exactly as do the autosomes and on that basis at least are perfectly normal. Since the only observable difference as regards the conditions of a cytological nature lies in the fact that the sex chromosome is paired in the female and unpaired in the male, MOHR's conclusion is a very natural one. It is that „die Formeneigentümlichkeiten, welche das Monosom in der Spermatozogenese darbietet, davon abzuleiten sind, daß es ohne Partner die Prozesse durchmachen muß, die zur Reduktion der Chromosomenzahl führen“. A similar conclusion has been arrived at by many other workers.

To hold the lack of a partner responsible for the heteropycnotosis of the monosome in the males of Orthoptera is of course only one logical step removed from the conclusion that heteropycnotosis may also result from the fact that the members of a pair (like the XY pair) are not homologous. Both hypotheses would be covered by the statement that heteropycnotosis of a chromosome is due to the lack of a homologous partner.

It must be confessed that this does not take us very far into an analysis of heteropycnotosis. Such as it is, the conclusion is supported by a great deal of affirmative evidence, but before even such a modest step in advance is accepted it may not be out of place to examine this evidence. There is no need here to mention the numerous cases which duplicate the Orthoptera in showing heteropycnotosis of the sex chromosomes in the heterogametic sex only. Evidence other than this but with a more or less direct bearing on the question may be given as follows:

Heteromorphic pairs of autosomes:—CAROTHERS ('13) first described in the Orthoptera *Brachystola* and *Arphia* a chromosome pair the partners of which are unequal in size. In the preparatory phases of the first spermatocyte this pair is condensed earlier than the other autosomes (fig. 6 A), although not quite as early as the unpaired X chromosome. Despite the inequality of this heteromorphic pair, a tetrad is formed and this is easily recognized because of its unsymmetrical shape. In *Arphia* another pair of autosomes also undergoes a condensation which is only slightly less precocious, but in that case no obvious inequality in size

is apparent between the two partners. Similar to this last named case is that described by ROBERTSON ('16) in *Acridium ornatus*, but here no thorough analysis was made. However, evidence of this nature supports the general thesis that heteropycnosis occurs when no homologous partner is available.

**Supernumeraries:** Closely related to the preceding is the behavior of supernumeraries. Wherever analyzed, these behave just like unpaired chromosomes or unequal pairs in that they undergo heteropycnosis. This is true for instance in *Metapodius* (WILSON, '07 c, '09 b), *Tettigidea* (ROBERTSON, '17), and *Diabrotica* (STEVENS, '08). But the most pertinent analysis was made by CARROLL ('20) in the case of the supernumeraries of *Cannula*. He found that different cells of the same testis showed either one or two supernumeraries. If only one supernumerary was present it condensed precociously just like an unpaired X, while if a cell contained a pair of supernumeraries no heteropycnosis was observable and both behaved like the paired autosomes.

**Polyploidy:** Evidence based on instances of polyploidy is not conclusive. If heteropycnosis occurs when a chromosome has no homologous partner but as is usually assumed does not occur when such a partner is present, then polyploidy should provide test cases. Thus if the chromosomes of an XO or XY male are doubled, each of the sex chromosomes is represented twice, that is to say it has an homologous partner. Unfortunately few cases of polyploidy have been examined with this question in mind. PAINTER ('25 b) reported that in the human male a chromosome nucleolus representing the XY pair is present during the growth stages of the spermatocytes, but in tetraploid germ cells it can not be found. He therefore concluded that "when two x chromosomes are present, they undergo synapsis and behave otherwise as the autosomes do". But this does not concur with BOWEN's findings ('22) according to which tetraploid spermatocytes of *Euschistus* show heteropycnosis of the X and Y, even though each of these is twice represented. Polyploidy therefore does not furnish conclusive support for our thesis.

**m chromosomes:** The nature of m chromosomes is not clear, but their behavior is of some interest in the present connection. As far as cytological observations go, the two m chromosomes as observed in the Hemiptera are exactly alike in size and configuration, but it must not be forgotten that their diminutive size renders the study of their structure very difficult. In *Anasa tristis* and *Chariesterus* they behave just like equal pairs of autosomes and condense from diffused masses in the same way and at the same rate as such autosomes (fig. 6 c). But in other instances this is not the case and in *Archimerus calcarator* where likewise no cytological difference in the structure of the two m chromosomes is observable, both condense distinctly in advance of the regular autosomes. The same may be said of *Alydus pilosulus* where however a slight variation in the rate of condensation may be observed in different individuals (fig. 6 b). Just as in the case of externally similar pairs of autosomes which undergo heteropycnosis, it may be suggested here that the m chromosomes in these last mentioned cases are really not homologous. This is in a measure supported by the fact that they do not undergo synapsis like the autosomes but come together for a very brief time only at the moment of division. On the other hand, the m chromo-

somes of *Anasa* which behave just like the autosomes come together and meet for just as brief a period as those that undergo heteropycnotosis.

Cases of heterogamety in the female: In instances where a cytological demonstration of heterogamety in the female and homogamety in the male is possible, it might be expected that heteropycnotosis occurs in the former. Reports of earlier observers on the cytology of the Lepidoptera which gave accounts of condensed sex chromosomes in the spermatogenesis (STEVENS, '06; DEDERER, '07; DONCASTER, '11, '12) were

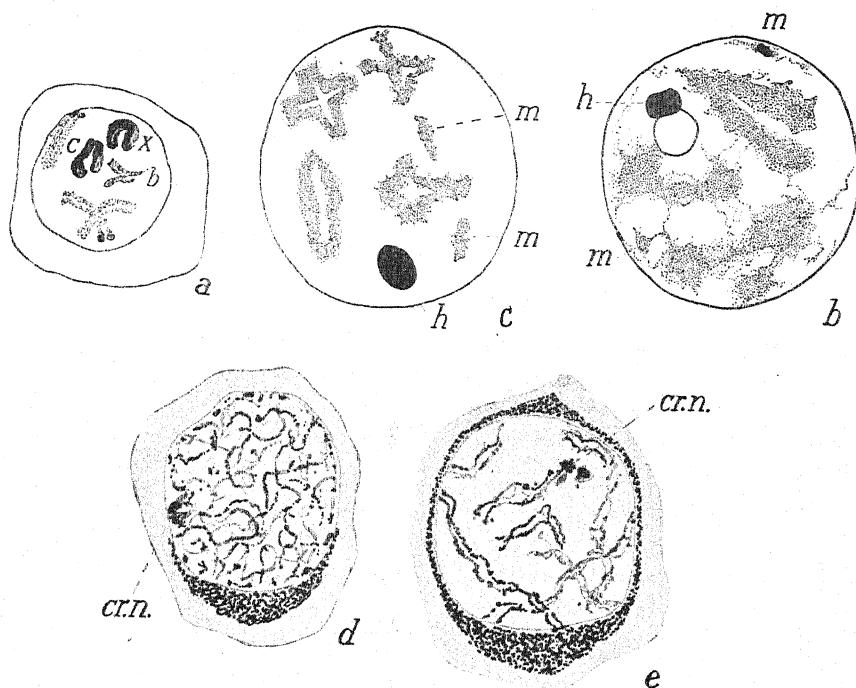


Fig. 6. *a* *Arphia simplex* (CAROTHERS, '13)—Growth stage in spermatocyte (*c* = precocious autosomal tetrad; *b* = fragment of another precocious autosomal tetrad). *b* *Alypus pilosulus* (WILSON, '05b)—Middle of growth period in first spermatocyte, showing condensed *m* chromosomes and *X* with attached plasmosome. *c* *Anasa tristis* (WILSON, '05b)—Condensation stage of first spermatocyte showing diffuse *m* chromosomes and condensed *X* (*h* = *X* chromosome). *d* *Cicada tibicen* (SHAFFER, '20a)—Oocyte in preleptotene stage showing two chromatin nucleoli (*cr.n.*). *e* Oocyte in strepsitene stage showing two chromatin nucleoli (*cr.n.*).

apparently all based on insufficient evidence. However the same may be said of DONCASTER's account of a chromosome nucleolus in the female. In *Phragmatobia*, *Talaeporia*, and *Fumea*, where SEILER has shown that the female certainly shows the XY (in *Phragmatobia*) or the XO condition, no heteropycnotosis was observed (fig. 34a). No reliable evidence either for or against heteropycnotosis in the female birds is available. Although there is here no support for the general thesis, it must be pointed out that our knowledge of the cytology and sex chromo-

somes in these two groups is hardly sufficient to justify any final conclusion.

Heteropycnotosis in the homogametic sex: Thorough investigations of the chromosome conditions in the homogametic sex (i. e. the female in nearly all cases) are few in number as compared with investigations of a like nature in the heterogametic sex. The great majority of such work supports the thesis here under discussion, in that no heteropycnotosis of the sex chromosomes is observable. There are however a few cases that seem to represent exceptions. FOOT and STROBELL ('11) described a chromatin nucleolus in the oogonia of *Protenor* and concluded that in some cases this represents the two largest chromosomes (i. e. the sex chromosomes). But they found also that in other instances, not only the sex chromosomes but also all the autosomes were evolved from this chromatin nucleolus. It is now quite probable that the latter observation is the only correct one and that they were dealing with a karyosphere.

No special mention need be made of cases like that of oocytes of *Gryllus* (BUCHNER, '09), *Pyrrhocoris* (HENKING, '92; GUTHHERZ, '07), and the cat (v. WINIWARTER and SAINMONT, '09), in all of which heteropycnotosis of the sex chromosomes was reported. In all these cases other workers contradicted such findings and BUCHNER, GUTHHERZ and v. WINIWARTER have themselves given up their earlier interpretations.

Not so certain is the status of a few other cases. STEVENS ('06) reported that the X chromosomes in the oocytes of *Aphrophora* undergo heteropycnotosis and although she may not have clearly differentiated between sex chromosomes and a true nucleolus, the case should be reexamined. PAYNE's results ('12b) seem to show that in *Galgulus* (*Gelastocoris*) the four pairs of X components in the female, undergo heteropycnotosis during the early growth stages in the oocytes. But it must be pointed out that these compound X chromosomes are located in a large plasmosome during this period and that special conditions are presented thereby. More recently SHAFFER ('20b) reported two chromosome nucleoli in the oocytes of *Cicada*. These are observable before the leptotene stage but then disappear only to reappear in the diplotene phases (fig. 6 d and e). SHAFFER does not seem to be certain, but is inclined to regard these chromosome nucleoli as the condensed X chromosomes of the female. All these rather inconclusive cases belong to the Hemiptera. Under the Coleoptera two other cases may be mentioned. WIEMAN ('10) found a condensed, bipartite body in the growth stages of the oocytes of *Leptinotarsa*, but gave little evidence regarding its exact nature and behavior. GOLDSMITH ('19) described two chromosome nucleoli in the oogonia of *Cicindela* and also two condensed bodies in the oocytes which he regarded as sex chromosomes (2 X<sup>I</sup> and 2 X<sup>II</sup>). But here again, the evidence does not permit a final conclusion. Finally should be mentioned the cases of the nematode *Heterakis* where GULIK ('11) described heteropycnotosis in both sexes, and of cattle in which WODSEDALEK ('20) reported a similar condition.

It is evident that all these cases do not seriously affect the conclusion that heteropycnotosis does not occur in the sex chromosomes of homogametic animals. Nevertheless it seems very important so reconsider all these forms with this particular point in mind, since an ana-

lysis of possible exceptions may throw more light on the problem than any number of confirmations of the general thesis.

Hermaphroditism: Cases of hermaphroditism in which no heteropycnotosis is observable in any individuals of the species concerned can furnish no data that bear directly on the present question. In at least two instances however pertinent information is available.

The hermaphroditic individuals of *Angiostomum* (BOVERI, '11; SCHLEIP, '11) develop from fertilized eggs with 12 chromosomes. They are primarily females with two X chromosomes and as might be expected there is no heteropycnotosis of these sex chromosomes in the oocytes. However, in the spermatogenesis of the same animal, there is heteropycnotosis of two chromosomes in the growth stages of the spermatocytes — although this does not occur quite simultaneously in both chromosomes. Since the males in most other nematodes have given evidence of being heterogametic it does not seem unfair to assume that in the hermaphrodites of *Angiostomum* the heteropycnotosis observed in male germ cells is related to heterogamety. It has been suggested that such a condition might be brought about by an alteration in one of the two X chromosomes basically present so that in the male cells there is found an XY instead of the original XX condition. With such an assumption of a change in one X, the two sex chromosome are of course no longer homologous, and heteropycnotosis therefore is based on the same factor as that assumed in our main thesis.

Another pertinent case is that of *Perla*, although this is not an instance of functional hermaphroditism. JUNKER ('23) found that in the structures which seem to represent an ovary in the males, the chromosomes which are typical of true male organs are also present. Therefore this so called "male ovary" carries a compound X (of two components) without a partner. In the true female germ cells, where a pair of compound X chromosome is to be found, no heteropycnotosis occurs. On the other hand, there is a marked heteropycnotosis of the single compound X in the growth stages of spermatocytes. This then is just what might be expected. However, in the "male ovary" where, as in typical male organs and germs cells, the compound X has no partner, little or no heteropycnotosis takes place (fig. 22). If JUNKER's observations are correct therefore, this case furnishes contradictory evidence to our thesis, for despite the lack of a partner for the sex chromosome, no heteropycnotosis occurs in certain of the cells.

Special cases: Here may be mentioned the cases of the males of certain Aphididae. In the cases considered by von BAEHR ('08, '09) no heteropycnotosis was observed in the spermatocytes of the males, although they seem to carry sex chromosomes without homologous partners. The figures given by MORGAN ('15) in his account of *Phyllaspis coweni* however show what appears to be a chromosome nucleolus in the early growth stages of the primary spermatocyte. MORGAN however did not analyze this body. After the first spermatocyte division the evidence is clearer, and before the second division is initiated, the tendency toward heteropycnotosis in the unpaired X is quite noticeable.

If all this evidence is summed up it is fairly clear that no conclusive case against our thesis is available. Generally speaking it still holds that heteropycnotosis occurs in chromosomes that have no homo-

logous partner. Evidence against this conclusion is with few exceptions counterbalanced by other evidence from different sources or else is based on instances which present very special conditions. But as has been implied already, such a conclusion does not go very far in uncovering the underlying causes of heteropycnosis.

However, one further step is possible on this basis. Among the many forms in which sex chromosomes can not be identified at all, there are a few in which genetic evidence justifies the conclusion that one sex is heterogametic as in all cases where sex chromosomes have been cytologically demonstrated. That is the case for instance in several species of fishes, where WINGE ('22 b) and AIDA ('21) have shown that in at least one pair of chromosomes of the male the genes are not exactly equivalent — in other words these animals are heterozygous for certain genes. The fact that no heteropycnosis occurs (WINGE, '22a) in these males demonstrates clearly that heterozygosity of genes does not constitute the inequality in a pair of chromosomes that would bring about heteropycnosis. Such inequality or lack of homologousness must therefore rest on something else, either in addition or independently. It may be suggested that a *loss* of certain genes would here furnish a promising subject for consideration. Whether this loss takes the form of a disappearance of certain parts of the chromosome involved, or whether it makes its presence felt as a deficiency (BRIDGES, '17) in which certain genes are absent as far as their genetic influence is concerned, is perhaps of little importance. The latter explanation would have to serve in those cases in which an XY pair is apparently identical in size, and still undergoes heteropycnosis. Such losses of genes may very well disturb the reactions that must occur between the chromosomes of each pair at certain stages, and it is possible that the greater the loss the more accentuated would be the heteropycnosis.

But it must also be pointed out that heteropycnosis probably rests on more than one factor. This is demonstrated by the way in which it occurs in a few exceptional cases. In *Enchenopa* (KORNHAUSER, '14) there is an unequal XY in the male and this pair undergoes heteropycnosis in the preparatory stages of the spermatocytes. However it is to be noted that in this case the X condenses distinctly in advance of the Y (fig. 33). Again, in *Tenodera* (OGUMA, '21) at a corresponding stage the Y remains condensed while the compound X forms threads (fig. 21). Finally in *Pseudococcus* (SCHRADER, '23a) five chromosomes undergo heteropycnosis while the remaining five do not (fig. 32). Only one conclusion seems valid in these cases at the present time. Heteropycnosis can not rest solely on the fact that normal interaction is hindered or prevented by inequalities in the chromosomes concerned, but it must also depend to some extent on the constitution of the individual chromosome. Without this last provision heteropycnosis should manifest itself alike in any two members of an unequal pair.

As bearing on the nature of heteropycnosis in sex chromosomes, mention should also be made here of the consideration of FICK ('07) and GUTHHERZ ('22). The former suggested that heterochromosomes in general may have a chemical constitution different from that of the autosomes and that therewith they also exert a different influence on the metabolism of the cell. GUTHHERZ who regards this idea sympathet-

tically, reviews it in connection with his analysis of a heterochromosome in the mouse. The greater amount of nucleolar substance which arises from the heterochromosome in that animal leads him to conclude that it must be more active chemically, while its spatial separation from the rest of the autosomes suggests to him a higher osmotic pressure in its vicinity. But although it must be admitted that this is a step in the right direction, the bases for GUTHERZ's conclusions are not yet firmly established.

All in all then we know astonishingly little about the cause of heteropycnosis. We know that it nearly always occurs when any chromosome has no homologous partner, but why it occurs under such conditions is still an unsolved question. Its answer no doubt involves a much more thorough knowledge of the structure and physiology of chromosomes than we now possess.

## SECRETION

The interrelations of the various elements in the cell are to a large extent still obscure. It is to this fact that our lack of knowledge regarding the various inclusions that are usually called plasmosomes is to be attributed. Such bodies have repeatedly been observed in intimate association with the sex chromosomes and on such observations have been based various hypotheses bearing on the physiology of the latter.

In considering such hypotheses, it must be pointed out however that autosomes also have been described as more or less constantly associated with certain bodies during preparatory stages. Thus PINNEY ('08), CAROTHERS ('13, '17), WENRICH ('16, '17), and GELEI ('21) have described such association, and usually applied the term "polar granules" to the extra-chromosomal structures. When these first appear they are in the form of small granules that take a chromatin stain, but WENRICH has observed that such polar granules may become enlarged, stain less intensely, and take on the appearance of true plasmosomes (fig. 18). It is impossible to treat here the numerous and scattered observations that have been made by others on the relationship of the chromosomes to cellular inclusions, but various aspects that are more directly connected with the sex chromosomes may be touched briefly.

Working on the spermatogenesis of *Blatta germanica*, WASSILIEFF ('07) described two nucleoli which originate from the division of a single body. During the preparatory stages of the spermatocytes both nucleoli contribute to the mitochondrial mass situated outside of the nucleus, there being an actual stream of nucleolar material in that direction („Abströmnungsprozeß“). The smaller nucleolus is entirely used up in this manner, but of the larger a portion still remains when the autosomal tetrads undergo final condensation. From this remnant and the stream of its material still inside of the nucleus, is formed the X chromosome. BUCHNER ('09) described a very similar process and origin of the X chromosome in several other Orthoptera, but was inclined to believe that the X arose almost entirely from the intranuclear stream of material present when the „Abströmnungsprozeß“ is stopped, and not from the rest of the still solid nucleolus. Both of these accounts have

been subjected to much criticism. MORSE ('09) could find no such phenomena and MOHR ('15, '16) has suggested that the stream of material observed by both of these workers represents nothing but the two attenuated ends of the unpaired X chromosomes, which like the autosomal threads become polarized during the bouquet stage (fig. 3 and 4). Although MOHR seems to have given the real explanation of the matter, the fact remains that too many observers have observed the association of sex chromosomes and plasmosomes to dismiss offhand the possibility of a connection between them.

Among the many cases in which a plasmosome is superficially attached to a sex chromosome (fig. 6 B) may be mentioned several Hemiptera (MONTGOMERY, '01b, '06; WILSON, '05a, '05b), *Aphrophora* (BORING, '07), *Anisolabis* (RANDOLPH, '08), and several Orthoptera (DAVIS, '08; SCHELLENBERG, '15) in addition to those already mentioned. As a rule such a plasmosome becomes separated from the X before the final condensation of the tetrads and then disappears. Similarly AGAR ('23) and GREENWOOD ('23) both described a plasmosome which is attached to the fused X and Y chromosomes during the preparatory stages of the spermatocytes of certain Marsupialia (fig. 40 B). The appearance of this plasmosome suggested to AGAR that "it is the persistent part of the bivalent from which the chromatin has flowed away into the rounded mass which forms the condensed sex bivalents: this appearance is strengthened by the fact that sometimes rounded granules or drops of chromatin are left in the plasmosome. In other cases it is pearshaped and is attached by its neck to the bivalent, irresistably suggesting that it has been squeezed out of the contacting chromosomes like a viscid fluid from a narrow aperture". The secretion or extrusion of a plasmosome was described also by GUTHERZ ('22) in the case of the mouse and rat (although GUTHERZ does not regard the heterochromosome there as a sex chromosome). PAINTER ('24a) also described a process (in *Didelphys*) in the course of which the sex chromosome nucleolus is separated into an oxyphilic and a basophilic portion, but contrary to most other authors believed it to be an abnormal development.

It is very possible that cases such as those just mentioned differ in no significant way from those in which sex chromosomes are partially or entirely imbedded in a plasmosome instead of being superficially joined with it. An X chromosome partially imbedded in a plasmosome has been described by STEVENS ('06a) in *Anomoglossus* spermatocytes, while in *Blepharida*, *Odontota* (STEVENS, '06a) and *Calliphora* (STEVENS, '08a) both an X and a Y are similarly imbedded. Cases in which all the components of a compound X are found inside of a plasmosome have been described in several Hemiptera (Reduviidae) by PAYNE ('08, '09a, '09b, '10). The inference ist natural that we are dealing here with a karyosphere or amphinucleolus which is merely more restricted than the karyospheres in which are included all the autosomes as well as the sex chromosomes (fig. 7). But the exact relation of the plasmosomic material to the sex chromosomes is still a mooted question. GOLDSMITH ('16) suggested that in *Pselioides* where the four components of the X chromosome are imbedded in a large plasmosome during certain stages of the spermatocytes, the plasmosomic material is identical in substance with the linin found in the more general nuclear

space, that this linin substance merely accumulates around the compound X, and that therefore the plasmosome has the same function that has been ascribed to the linin network, namely to support the chromatin material.

If the "polar granules" already mentioned are really related to plasmosomes of the kind here in question, a possible significance may attach to the fact that such polar granules when attached to autosomes seldom attain the size of the plasmosomes associated with sex chromosomes. This may indicate that the sex chromosomes are more active

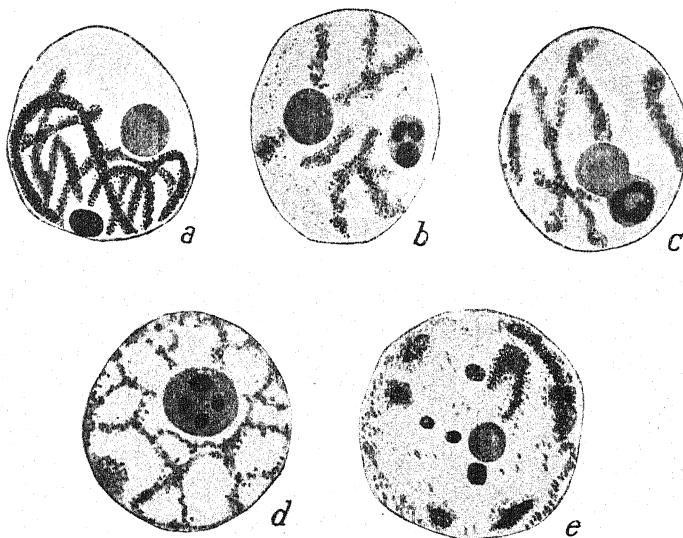


Fig. 7. *Prionidus cristatus* (PAYNE, '09a)—*a* Spireme stage following synapsis in first spermatocyte, showing compound sex chromosome and plasmosome. *b* Breaking up of sex chromosome, with plasmosomic material around it. *c* Fusion of plasmosome with compound sex chromosome. *d* The four components of the compound X separated from each other. *e* Prophase, showing stage in which the components of the X have left the plasmosome.

in their chemical processes, and such a conclusion is indeed reached by GUTHERZ ('22) in regard to the heterochromosome that he described in the mouse. Although this possibility is not to be discarded without further investigation, it may be well to suggest that hypotheses directly opposed to that of GUTHERZ might be based on the same observations. Thus it seems possible that there is some interaction between the chromosomal constituents and some other cell constituent. In the case of the autosomes this interaction occurs smoothly, but the sex chromosome reacts more slowly and as a consequence there is an accumulation (the attached plasmosome) of the extra chromosomal constituent. But such a possibility is suggested merely to show how helpless we are in our hypotheses of chromosome physiology without additional knowledge of a basic sort.

Finally, it must not be forgotten that in some cases at least there is a possibility that we are dealing with nothing but an artifact. The plasmosome may indeed be squeezed out of the sex chromosomes as AGAR suggests, but this may be the result of the action of the fixing fluid on the chromatin.

## THE RELATION OF SUPERNUMERARIES TO SEX CHROMOSOMES

The occurrence of supernumeraries or extra chromosomes concerns us chiefly because of the possibility that they are in some cases derived from the sex chromosomes or else have an origin similar to that of sex chromosomes. Such supernumeraries have been studied especially by WILSON in the course of several of his earlier investigations and his conclusion in regard to their origin may best be summed up as he does himself ('25a), that is, that they arise through "the failure of sister-chromosomes to separate in an ordinary equation division" or "the failure of two synaptic mates to separate in the reduction division and their passage together to one pole of the spindle".

A similar origin may be ascribed to the extra autosomes in such cases as the 15 chromosome mutants of *Oenothera*, the various extra chromosome forms of *Datura*, and forms of *Drosophila* with an extra fourth chromosome. The presence of supernumerary autosomes may have a profound effect on sex determination and this will be considered later, but at present only supernumeraries which may stand in some relation to sex chromosomes are under discussion.

In this connection may be mentioned especially the case of *Metapodius* (WILSON, '07a, '07b, '07c, '09b, '09e, '10a). It was found that the normal diploid number of chromosomes, which is 22, may in some individuals be increased to as high as 28. The extra chromosomes betray their relationship to sex chromosomes in undergoing heteropycnosis like the X and Y and in uniting with these sex chromosomes to form a single chromosome nucleolus during the preparatory phases. Such behavior is by no means general in all extra chromosomes, for supernumerary or extra m chromosomes never become united with the sex chromosomes. In the first spermatocyte division the supernumeraries here in question divide equationally just like the sex chromosomes of *Metapodius*, while in the second spermatocyte division they again simulate the X and Y in passing undivided to one pole. In most cases their distribution in this last division follows that of the Y and often the supernumeraries may actually be coupled with it at this time (fig. 8). Since WILSON had already discovered a specimen lacking a Y chromosome altogether, without any visible effect on the animal, and since even the greatest number of supernumeraries similarly had no influence on the morphology of the animals, he suggested that not only is there a good deal of evidence that supernumeraries are closely related to sex chromosomes, but that they may be still further diagnosed as partaking more of the nature of the Y than the X. This would of course receive support from his findings that in most cases the supernumeraries accompany the Y and not the X in the heterokinetic division. WILSON's hypothesis that such extra Y chromosomes arise through non-disjunction

was later strengthened by direct observation (WILSON, '09 e) on individuals of *Metapodius* which showed the Y going to the same pole with the X in the heterokinetic division. Finally WILSON pointed out that supernumeraries smaller than the Y are probably degenerating—a process which would not be attended by any other visible results since his earlier findings had already demonstrated that in *Metapodius* the lack of even the regular Y has no effect on structure.

The supernumeraries observed by WILSON ('07 c) in *Banasa calva* probably have the same origin as those of *Metapodius*. The status of the supernumeraries that STEVENS ('08 b) described in *Diabrotica soror*

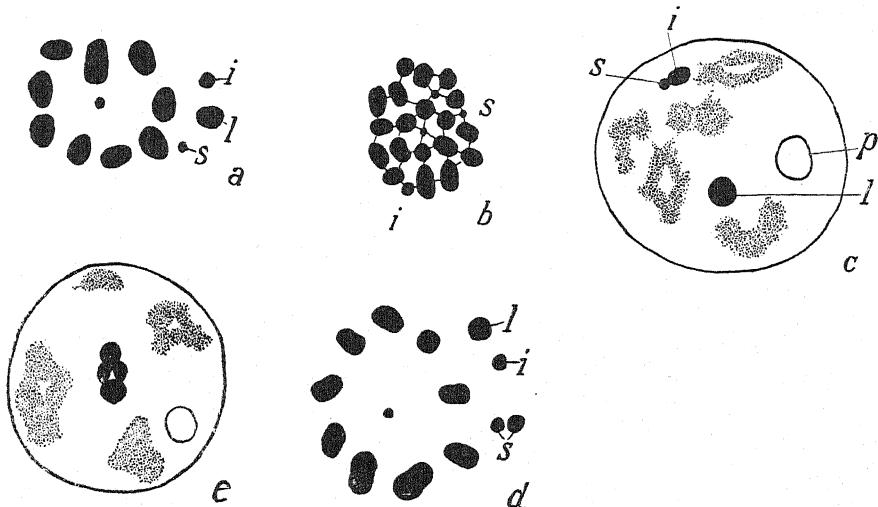


Fig. 8. *Metapodius terminalis* (WILSON, '06)—a Metaphase of first spermatocyte. b Spermatogonial metaphase including one supernumerary. c Condensation stage of first spermatocyte showing supernumerary attached to Y. d Metaphase of first spermatocyte showing two supernumeraries. e Condensation stage of first spermatocyte showing two supernumeraries attached to the XY pair ( $p$  = plasmosome;  $s$  = supernumerary;  $l$  = X chromosome;  $i$  = Y chromosome).

is however not so clear. It is true that as in *Metapodius* they simulate the unpaired sex chromosome of the male in undergoing heteropycnosis in the preparatory stages of the first spermatocytes, and also in passing undivided to one pole in one of the meiotic divisions. But it is plain that here the supernumeraries can not represent Y chromosomes that can be traced to a process of non-disjunction, since the males of *Diabrotica* carry no Y. On the other hand a very striking feature of the case lies in the fact that when supernumeraries are present the normal X of the male often elongates and forms a short thread in the growth stages, whereas without supernumeraries it remains condensed and spherical. This behavior suggests that the supernumeraries are in some way homologous to the X, and that as a consequence the latter approaches more closely to the behavior of the paired autosomes or else the paired X chromosomes of the female. At the same time it is clear that if the

supernumeraries are actually related to X chromosomes, they have lost the properties that influence sex or any other character. A similar explanation may account for the extra chromosome found by ROBERTSON ('17) in one male of *Tettigidea parvipennis*. This supernumerary was found to behave in every essential like the X (which in normal males is unpaired). Its distribution in the heterokinetic division is entirely at random, and it may go to the same pole or to the pole opposite to that of the regular X. Since its presence evidently had no noticeable effect on the male in question, it seems fair to conclude with ROBERTSON that it may represent an X that has lost its sex genes. Possibly that is borne out by the demonstrable fact that it is shorter than the normal X.

The evidence is thus fairly strong that supernumeraries may in some instances take their origin from sex chromosomes. But how they become non-functional with respect to sex determination is a problem in itself, and perhaps one not different basically from that in which the nature of the Y chromosome is involved.

## COMPOUND SEX CHROMOSOMES

Mention has already been made of the fact that in some forms the X chromosome is represented by more than one element. A compound Y is apparently much more rare, and except for *Pseudococcus* (SCHRADER, '21, '23 a) in which we are still not certain of dealing with a Y chromosome at all (fig. 32), and possibly *Odontota* (STEVENS, '06 a) where certain individuals perhaps present a compound Y as an abnormality, there are on record only the instances of *Rumex* (KIHARA & ONO, '23 a, b; SINOTO, '24) and, if SEILER's interpretation is correct ('13), *Phragmatobia* (fig. 34). In *Rumex* the Y has two components, while in *Phragmatobia* the heterogametic female has a W (which corresponds to the Y of forms in which the male is heterogametic) which is single at the beginning of the meiotic divisions but may break up into two or more components in the early development.

Although in most known cases of the compound X a Y (always a single element) is also present, there are some well established instances in which the compound X has no partner— for example *Syromastes* (WILSON, '09 a, d) and several species of *Lacertilia* (PAINTER, '21 a) (fig. 38). But with or without a partner, the compound sex chromosome behaves in all essential respects like the more common single sex chromosome. Wherever a more detailed analysis has been possible, the components of the compound X have as distinct an individuality as unit chromosomes and their number and relative size is constant except during the phases when they may fuse. The behavior that characterizes unit sex chromosomes during meiosis is found also in the case of compound sex chromosomes. If a Y is present the brief apposition often noted as taking place between unit X and Y chromosomes, may occur here also (as in *Blaps*—NONIDEZ, '20), while the more complete union as evinced by the combination of X and Y in a single chromosome nucleolus during the preparatory stages is paralleled by such cases as *Tenodera* and *Paratenodera* (OGUMA, '21). In the reduction division, even in those cases where the components of the X have remained

separated throughout, they act as a unit and always pass to the same pole. It is preceding this division that the relation of the various components to each other is most often betrayed, for they then very often form groups of a fairly definite configuration and show that a bond of some sort exists between them (as shown by Payne in several Reduviidae) (fig. 30). But even if no such configuration is observable, it is clear that during the reduction division at least the components of the compound X are not entirely independent of each other. Without a bond of some sort random segregation might be expected to occur and the resultant gametes should then carry a varying number of X components—something which is not found to be the case under normal conditions.

This collocation or fusion of X components during meiosis has an indirect bearing on the analysis of the forces that are instrumental in bringing together the partners of ordinary chromosome pairs during synapsis. As usually presented, such pairing is held to be due to the fact that the two participating chromosomes are homologous to each other—a rather noncommittal statement. A consideration of compound chromosomes however advances us one little step. If the forces instrumental in pairing are identical with the forces that cause collocation of the X components during meiosis, it may safely be assumed that the homology here in question does not rest on the fact that the two chromosomes carry corresponding or allelomorphic genes. The nature of most compound X chromosomes makes it almost certain that they are the parts of an originally single chromosome and therewith falls the possibility that identity of genes carried in them can be held accountable for collocation.

The belief that the sex chromosome of several components arises in most cases from a single or unit chromosome is based primarily on such cases as that of *Notonecta* (BROWNE, '10, '13, '16). In several species of this genus a more or less typical XY pair is found in the male, but in *N. indica* the X chromosome shows certain special features. Thus during meiosis it shows constrictions which cause it to appear as a chain of chromatin bodies. The latter never exceed six in number, and typically there are five smaller and one large element (fig. 28). Although the separation of these elements from each other never becomes complete, the true compound condition is often very closely approached in those instances in this species where only the merest thread connects adjoining elements. A slightly different aspect is presented in *Phylloxera caryaecaulis* (MORGAN, '09, '12, '15) where the X is an apparently single or unit chromosome for the greatest part of the cycle, but at time breaks up into two smaller elements and thus betrays its compound character (fig. 31). In most other cases the conditions are reversed and the components of a compound X are separated at all stages except meiosis. Cases in which the X shows two components for all or the major part of the cell cycle are found in *Syromastes marginatus*, *Agalena naevia*, *Lepisma domestica*, several *Lacertilia*, *Thyanta calceator*, *Fitchia spinulosa*, *Rocconata annulicornis*, *Conorhinus sanguisugus*, *Tenodera superstiosa*, *Paratenodera aridifolia*, *Belascaris triguetra*, and *Ganguleterakis spumosa*. An X of three components has been described in three Reduviidae (*Prionidus cristatus*, *Sinea diadema*, *Pselliodes cinctus*); an X

of four elements in *Pnirontis modesta* and *Gelastocoris oculatus*; an X of five elements in *Acholla multispinosa*, *Sinea rileyi*, *Ascaris lumbrioides*, and possibly various species of *Pseudococcus*; an X of six elements in *Ascaris canis* (fig. 13); an X of 8 elements in *Ascaris (Contracaecum) incurva*; and finally an X of possibly even more than 8 elements in *Ascaris megalcephala*. When all these cases are considered in detail, WILSON's conclusion ('25a and earlier) that the X even in typical cases consists of several components but that these are normally firmly united, can become only more firmly established. The visibly compound X is then only a manifestation of a dissolution of the bonds that in other cases serve to make the X appear as a single chromosome.

It is however only fair to point out that although the origin of a compound X from a unit sex chromosome seems clear in most cases, there may be exceptions to this rule. Thus although in *Pseudococcus* there seems to be an X of five components, it is an exceptional feature of the case that these five components are all of exactly the same size (fig. 32). That, with the questionable nature of this so called X and certain other features creates the possibility that we have here only a simulation of the compound sex chromosome. As has already been pointed out (SCHRADER, '23a), each of the five elements in question may represent a unit chromosome, and therewith we have a slightly different condition than that here in consideration.

In no other connection is there so great a temptation to utilize known cases in the construction of "evolutionary series". Starting with the X in the unit condition, such a series can arrive by gradual steps at the condition in which the X is composed of many components. If the conclusion derived therefrom is that in all probability the compound X is basically a single chromosome no objection can be made since a detailed analysis only supports such a generalization. But it must be realized that such a series throws no light on how and at what rate the breaking up into components occurred.

It is perhaps unnecessary to mention that autosomes like sex chromosomes may at times betray a compound character. Usually the components of such autosomes are separated in the somatic divisions, but come together during meiosis (CAROTHERS, '13, '17; HANCE, '17, '18; SEILER, '22; SEILER & HANIEL, '21). It is not so certain that the meiotic chromosomes of the Hymenoptera belong here. It is true that such chromosomes break up into smaller components with great regularity after the meiotic period, but as in *Pseudococcus* the components are remarkably alike in size, and as in *Pseudococcus* we are not certain of the status of sex chromosomes in the species involved. To be sure it is quite possible that these cases deserve no special rank, but it also not entirely inappropriate to draw attention to their peculiarities.

## MULTIPLE CHROMOSOMES INVOLVING SEX CHROMOSOMES

The adherence one to another of chromosomes belonging to different pairs has been observed in a number of cases. The multiple chromosomes thus formed always involve certain definite members of the chromosome group, and usually show great constancy during certain phases

in any one individual or even species. We are concerned here only with those multiple chromosomes which include sex chromosomes, although the factors which bring about the formation of such combinations are no doubt identical with those instrumental in purely autosomal multiple chromosomes.

The clearest and most striking cases have been found among the Orthoptera. As early as 1901 DE SINETY described in several genera, notably *Leptynia*, the coupling of the X with one of the autosomes. Similar multiple chromosomes were found by MC CLUNG ('05, '17) in *Anabrus*, *Mermiria*, and three species of *Hesperotettix* (fig. 9). Although in most of these cases the coupling takes the form of an end to end attachment, this is not always the case. *Hesperotettix pratensis* for instance includes individuals in which certain cells show the X adhering to an extension of an autosomal tetrad and not its end, and a similar attachment has been observed in *Anabrus*.

It is of some interest to note that as MC CLUNG pointed out in 1905, the multiple chromosome in cases like *Mermiria bivittata* is apparently a permanent combination and no dissociation of the chromosomes involved occurs in any of the cells. This in turn implies that since in the Orthoptera the odd X of the males is always in the female producing gamete, the partner of the autosome to which it is so permanently attached is confined to the male line.

So far as the cytological evidence goes, the behavior of chromosomes involved in the multiples is not affected by the coupling. As a consequence we find that in the meiosis of the male the attached autosome undergoes all the preparatory changes that occur in its free partner and the other autosomes; that it forms with its free partner a typical tetrad and that the latter undergoes two maturation divisions of the normal type.

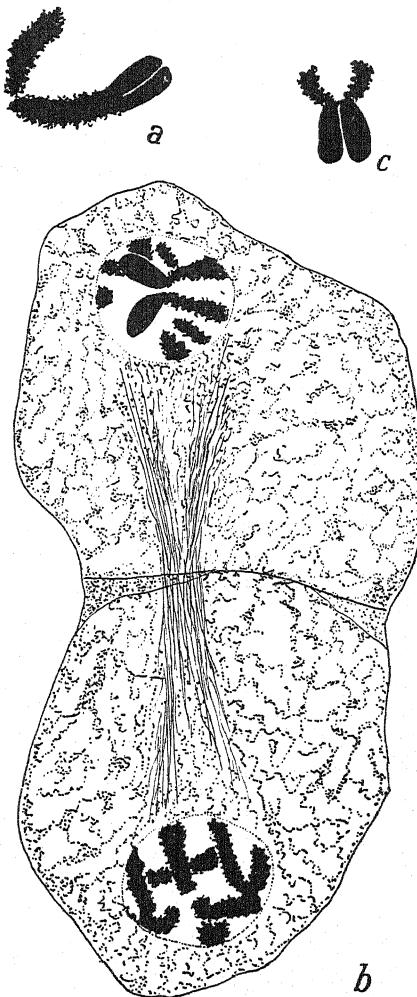


Fig. 9. *Hesperotettix speciosus* (MC CLUNG, '05) — *a* Hexad multiple chromosome in prophase of first spermatocyte. *b* Telophase of first spermatocyte division showing chromatids of multiple chromosome separated. *c* Multiple chromosome isolated.

The attached X which of course has no partner, is subject to heteropycnosis just as a free X would be, and divides in only one of the maturation divisions. The little evidence available indicates that the attachment of the X to an autosome is not confined to the males, for in the females where two X chromosomes are present, both are coupled with the autosomes corresponding to that involved in the male (in *Mermiria bivittata*).

In some other forms there also appear to be multiple chromosomes but the cytological features are not so well known, or are complicated by other circumstances. Thus the X of *Ascaris megalcephala* is united with an autosome in such a way that normally there is no indication of its presence, but the case is much complicated by the compound character of all the chromosomes. In *Anopheles punctipennis*, STEVENS ('11a) reported that the X and Y of the male are attached to a certain pair of autosomes, and as in case of the Orthoptera mentioned above, the character of the autosomes and sex chromosomes involved is not altered through the association (fig. 10). In *Necturus maculosus*, KING

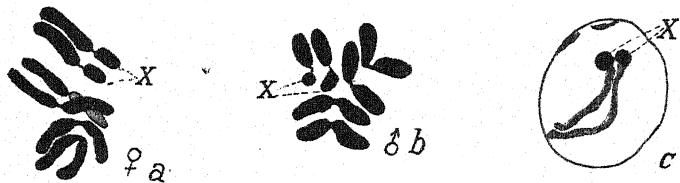


Fig. 10. *Anopheles punctipennis* (STEVENS, '11a)—a Oogonial plate with two multiples. b Spermatogonial plate with two multiples c Growth stage of first spermatocyte (sex chromosomes marked X without distinction).

('12) described in the spermatogenesis an autosomal bivalent of peculiar conformation. According to her interpretation it represents an autosomal tetrad with an X attached at one end and possibly a Y at the other. The evidence is manifestly incomplete, and the case merits further investigation. The case of *Blaps* (NONIDEZ, '20) may also be mentioned in this connection, for although WILSON ('25a) suggested that the male has in this case a compound X of four components opposed by a single Y, NONIDEZ himself was inclined to regard the peculiar complex in question as a single X united to four autosomes during meiosis (fig. 23 and 24).

As already stated multiple chromosomes involving only autosomes may also be formed (as in the cases of *Notonecta insulata*, *Hesperotettix speciosus* and *Chortophaga viridifasciata*). Correspondingly, multiple chromosomes composed of sex chromosomes only are encountered. Such cases have been discovered in *Drosophila melanogaster* by L. V. MORGAN (22, '25), ANDERSON ('25) and STURTEVANT (MORGAN, BRIDGES and STURTEVANT, '25). In all of them two X chromosomes are coupled and the multiple chromosomes thus formed are therefore composed of homologous chromosomes, in contrast to the cases mentioned previously. While the cytological evidence alone is sufficient to show that the two X chromosomes are attached to each other at one of their ends, the genetic data

furnish the additional information that it is the two so called right ends that are coupled. As might be expected, crossingover between the X chromosomes thus associated, is affected. In the same species STERN ('26b) has reported the interesting aberration of an X and a Y attached to each other (fig. 25 c).

Finally may be mentioned such special cases as that of *Physaloptera* (WALTON, '24) and *Gryllotalpa borealis* (PAYNE, '12b, '16). In the former both sexes during meiosis show a constant association between the sex chromosomes and a certain one of the autosomes, a feature especially striking at the time when the sex chromosomes lag on the spindle of the first spermatocyte and oocyte divisions. This behavior is not unlike that observed by GOODRICH ('16) in *Contracaecum*, but in the case of *Physaloptera* absolutely no bond of any kind is visible between the two chromosomes that form the association. It is to be considered of course that there is a possibility that these two chromosomes are simply subjected to the same influence which ordinarily induces lagging only in the sex chromosome. The nature of the associated chromosomes in *Gryllotalpa borealis* (fig. 20) is not sufficiently clear to justify even a conjecture.

It will be seen from the above considerations, that the factors which bring about the formation of multiple chromosomes of any kind, are still obscure. But it is also apparent from the progress made in the genetic analyses of the coupled X chromosomes in *Drosophila*, that in the future the tools of the geneticist may aid the cytologist considerably in the solution of this problem.

## PRECESSION AND SUCCESSION

In the heterogametic individuals of some species the sex chromosomes are characterized by a distinctive behavior in the heterokinetic division (the division in which there is a differential distribution of the sex chromosomes). This behavior, covered by the terms "precession" and "succession", is so striking that several observers have made it their chief and perhaps only criterion for the recognition of sex chromosomes. But such a proceeding is certainly not safe in view of the fact that other chromosomes may also, though less frequently, show precession or succession. Thus WILSON ('09b) states that in *Metapodius* the m chromosomes usually lead the way in the march to the poles in the first spermatocyte division, and among the Orthoptera are many instances in which autosomes lag behind or precede the main group during the meiotic divisions.

Although the behavior is thus not specific for sex chromosomes, its more general occurrence is not an indication that its occurrence is governed by accident. On the contrary, as far as the sex chromosomes are concerned, such exceptional behavior during heterokinesis if occurring at all is nearly always remarkably constant for any one species. Thus in the majority of Orthoptera the X of the males always precedes the autosomes to the pole in the heterokinetic division (fig. 3, 18, 19 and 20). On the other hand most Hemiptera show the sex chromosomes

lagging behind the autosomes in this division (fig. 2, 28 and 29). Exceptional species occur in both orders, and thus *Forficula* among the Orthoptera shows the X lagging while *Syromastes* among the Hemiptera is an example of precession. But whatever the behavior of the group as a whole may be, the separate species are quite consistent and constantly show only one of the alternatives — except for the case of *Vanduzea* (BORING, '07) in which apparently either precession or succession may occur.

None of the explanations advanced in connection with this behavior are fully adequate. Thus it may be assumed that in the meiosis of male Orthoptera, the X precedes the autosomes to the poles simply because it condenses sooner than they and is therefore ready for mitotic distribution at an earlier time. But heteropycnosis also characterizes the sex chromosomes of the males in Hemiptera, and there as already mentioned the more common phenomenon is lagging or succession.

Or, a succession may be brought about by the fact that for some as yet unknown reason the equational halves of the sex chromosomes are parted from each other only with difficulty. Thus *Photinus consanguineus* (STEVENS, '09a) shows the X dividing long after the autosomes have been divided, and although division finally occurs, there is the strong suggestion that the slightest further retardation would cause the X to enter only one cell (WILSON, '25a). However, this cause can not be universally responsible, for again in Orthoptera where no equational division of the X occurs in the first division and which therefore might be regarded as an extreme retardation in the separation of the equational halves of the X, precession and not succession is the common phenomenon.

To attribute precession or succession to the fact that the chromosomes involved have no equivalent partner and are therefore hindered in some way in following the normal type of division, is not striking very deeply for a solution. Certainly, the extremely irregular distribution of the chromosomes in the meiotic divisions of hybrids would tend to support such a hypothesis, and there it seems fairly certain that lack of homology is accountable. But it must not be forgotten that lagging for instance has been observed in the case of some chromosomes which are almost certainly partners — as for instance in the case of the two X chromosomes of the males of *Phragmatobia* (SEILER, '14). Indeed, neither pairing or any other meiotic phenomenon may be entirely responsible, for in *Tenodera*, OGUMA ('21) has described a lagging in the spermatogonial divisions.

A lagging of the large X chromosomes in the homogametic females of *Physaloptera* led WALTON ('24) to suggest that it is purely the mechanical difficulty involved in the division of a greater mass that might be responsible for some cases of lagging. But again, this can be true of only some of the cases since too many instances are known in which tiny sex chromosomes lag behind much larger autosomes and large sex chromosomes precede smaller autosomes to the pole.

Despite the volume of information on the question as a whole, it is thus quite evident that our knowledge of the deeper lying factors involved, is a very slim one.

## SIZE OF SPERMATOZOA AS AFFECTED BY PRESENCE OF SEX CHROMOSOMES

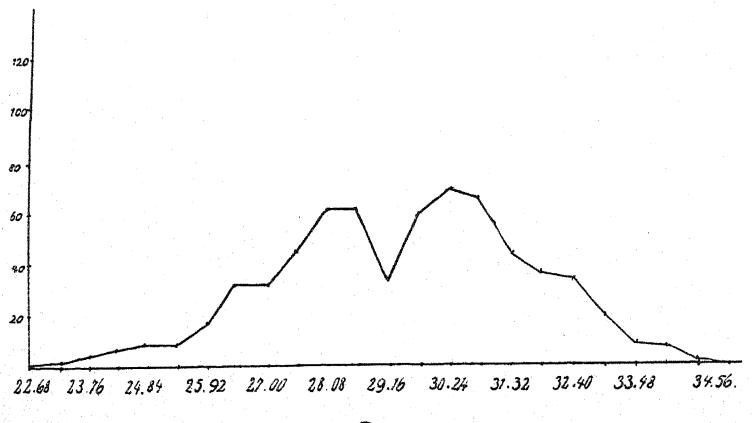
In cases where a cytological study of the meiotic divisions permits the conclusion that two kinds of gametes are formed, there is a possibility that this digamety may be reflected in some morphological way in the mature gametes. In very few instances only do the mature gametes show chromosomes, as in *Ancyra canthus* (MULSOW, '12). Chromosomes as such can therefore not serve as a basis for differentiating mature gametes, and efforts to distinguish two kinds of gametes have therefore taken another direction. In individuals showing either the XO or an unequal XY condition, it is clear that the cells after reduction must differ in the amount of chromatin carried. If this difference can be recognized in the mature gamete, a basis for differentiation is given. Measurements have been confined almost entirely to the spermatozoa, not only because the male is usually the heterogametic sex but also because it is generally assumed that all of the chromatin carried by the sperms is contained in the sperm head and is usually in a compact and dense condition, while another consideration lies in the fact that large numbers of sperms can usually be obtained.

Unfortunately a critical examination of most of the investigations of this kind is conducive to an attitude of scepticism. In the majority of cases only the length of the sperm heads is considered. There is no reason to doubt that using this measurement, the frequency distribution of the size groups of the sperms shows a bimodality in many cases (fig. 11), but that this is due to the presence or absence of an X or the unequal size of X and Y, is not always so certain.

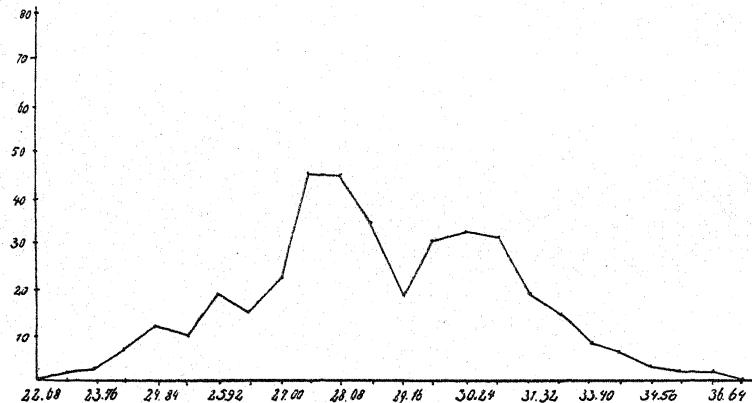
In instances like that of *Ascaris (Contracaecum) incurva* (GOODRICH, '16), in which a compound X constitutes a large portion of the total amount of chromatin present, its presence or absence may well be reflected in the size of the sperm head, and this expectation is realized. The bimodal curve derived from the measurement of the volumes of 600 sperm nuclei showed maxima having the ratio 1.4 to 1, and this result compares well with computations based on volumetric measurements of the two kinds of metaphase groups of chromosomes in the second spermatocytes (those with a compound X and those with the unit Y).

Reports of a dimorphism of spermatozoa in the vertebrates are founded less securely. GUYER ('09 b) was one of the first to claim that there are two size-classes of sperms and that the presence or absence of a sex chromosome is to be held accountable for their existence. This conclusion, based on his study of the spermatogenesis of the domestic chicken (*Gallus*), was however retracted in 1916. But GUYER's first findings received a whole series of substantiations in other vertebrates, the claims, as in GUYER's own case, being usually based on measurements of the length of the sperm heads. Here may be mentioned the work of WODSEDALEK ('13 b, '14, '20) on pigs, horses and cattle; MALONE ('18) on dogs; and more recently PARKES ('23) on rodents and man. Taking WODSEDALEK's investigation of the pig ('13 b), it is found that the curve plotted on the basis of measurements of the length of

sperm heads is distinctly bimodal, the two maxima showing the ratio of 1.2 to 1. On the basis of WODSEDALEK's own findings that the chromosomes carried in the two types of sperms are  $8 + X^I + X^{II}$  and 8 respectively, and that each of the two components of the compound X is only slightly smaller than the autosomes, this size dimorphism is just



a



b

Fig. 11. *Anasa tristis* (ZELENY & FAUST, '15a).—Frequency distribution of the length of sperm heads from *a* right testis, and *b* left testis.

about what might be expected. On the other hand, when it is considered that since that time HANCE ('17 b) has demonstrated that WODSEDALEK's counts are far from correct and that the haploid number is 20 and not 8 or 10 as submitted by WODSEDALEK, our faith in the interpretations of the latter worker can not but be weakened. Indeed, with the possible exception of WODSEDALEK's account of the chromosomes in cattle, a very similar objection can be upheld in connection

with the other cases of mammals in which dimorphism in the length of sperm heads has been correlated with sex chromosomes. The recent work of PAINTER especially has shown that in nearly every case the number of chromosomes actually present is considerably higher than that given by the earlier investigators of mammal chromosomes, and moreover that the sex chromosomes are usually by no means larger than the autosomes. Therewith it becomes manifest that the amount of chromatin in the sex chromosomes constitutes only a very small proportion of the total amount, and if it is considered that there is a perceptible amount of variation in size plainly due to other causes, the whole question gains a very dubious aspect.

In insects, where the chromosome conditions are better known, metrical studies on sperm heads have been reported by FAUST ('13), ZELENY and FAUST ('14, '15 a, '15 b), and ZELENY and SENAY ('15). Their general conclusion supports the view that sex chromosome differences are reflected in the length of the sperm heads (fig. 11). As in the cases of vertebrates, there can be no doubt that the dimensions of the sperms do vary and this point had been established as early as 1910 by MONTGOMERY. But even earlier ('98) this same author had called attention to the fact that the size of spermatocytes varies in different lobes of a single testis. This point has been taken up by BOWEN ('22 b) who demonstrated that the variation in the size of spermatocyte cells is considerable, and that the sperms produced from neighboring lobes may differ correspondingly. As BOWEN pointed out, factors such as these were not taken into account by FAUST and his fellow workers, although it is obvious that thereby a dangerous source of error is introduced.

A diversity in the size of spermatocytes and sperms has been mentioned also by BLACKMAN ('05 a) and BOUIN ('20, '22), neither investigator attributing this variation to the chromatin contained in sex chromosomes.

The whole subject is evidently not well settled. In cases where the sex chromosomes carry a great fraction of the total volume of chromatin, the sperms may well show by their size whether or not they carry an X, a Y, or no sex chromosome. In other cases however, complicating factors have plainly not been considered with sufficient caution.

## SYNAPSIS OF THE X AND Y CHROMOSOMES

That the X and Y chromosomes differ in some essential respects from the normal autosomes, is sufficiently borne out by the fact that they usually do not participate in the typical synaptene stages or the formation of tetrads. Nevertheless there are indications that the forces which bring about a conjugation of autosomes may also be present, to some extent at least, in the sex chromosomes.

Obviously in the case of the XO condition, no such manifestation can be expected. However, forms in which a Y is present have furnished some interesting observations in this connection. In many instances there is a distinct tendency for a coming together of the X and Y during the growth stages. The association may be a very temporary

one as in case of *Oncopeltus* and *Lygaeus* (WILSON, '09a, '12) where the more or less condensed sex chromosomes are in contact with each other during the synaptatene stages (fig. 2). In some cells of these forms no such union of the sex chromosomes takes place, but the union is too common to be merely accidental. The nature of the union is not clear, but apparently it is only a superficial contact in which the X and Y can always be definitely differentiated from each other. In other cases (fig. 12) the union that occurs during the growth stages of the meiotic period is a more intimate one (as for instance in *Didelphis*,—PAINTER, '24a) and the X and Y are contained in a single chromosome nucleolus. But again, cytology furnishes no evidence as to any possible interaction between the two sex chromosomes while thus united, although the joined X and Y may enter the primary spermatocyte spindle in the semblance of a tetrad. The inequality of the two partners is usually quite manifest in these structures and such tetrads need not necessarily indicate any preceding synapsis stages.

There appears to be no correlation between the behavior of the sex chromosomes in the preparatory stages and the actual meiotic divisions. Usually the X and Y have a fairly constant position with respect to each other in at least the metaphase of that division which is for them reductional. In most cases no relationship is apparent between them in the metaphase of their equation division. Thus in many Hemiptera where the first meiotic division is equational for the sex chromosomes, the latter are located at random and separated in the first metaphase plate even when they have been joined in the preparatory stages (fig. 8). It is only in or after the last anaphase period of this division that they come together. This contact is not broken until the second division has been initiated and the X and Y pass to opposite poles. In some instances this contact represents the only form of conjugation undergone by the XY pair.

In a corresponding way, if the first meiotic division is reductional for the sex chromosome pair, the X and Y take a definite position with respect to each other before this division is initiated even if they have been separated from each other throughout the preparatory phases.

It is a question whether the brief contact which the X and Y undergo in some cases while an actual division is in progress, is of a synaptic nature. Such a coming together is perhaps parallel to the second pairing of the autosomes of such forms as *Lepidosiren* (AGAR, '11). Here a perfectly typical conjugation of the chromosomes in pairs is followed by their separation, and a subsequent second pairing which occurs when the spindle is already formed. Just as in the case of the brief pairing of the X and Y chromosomes, the second pairing of *Lepidosiren* is almost immediately terminated by the separation of the partners in the division. Whatever the significance of the second pairing, it does not appear to be of the synaptic character that is to be observed in the first and typical conjugation, and it is to such a second pairing that the coming together of the X and Y on the spindle may perhaps be compared.

In only the most isolated cases has anything approaching typical synapsis been reported in the XY pair. Thus the X and Y of *Enchenopa* (KORNHAUSER, '14) after uniting end to end, bend around and come to

lie side by side. But despite the fact that these two sex chromosomes form fairly long threads it is doubtful whether a true synaptic process occurs, for KORNHAUSER observed that the X is always slightly more condensed than the Y at this stage (fig. 33).

Genetic evidence of crossing over between the X and Y would of course indicate some kind of interaction between them. In *Drosophila*

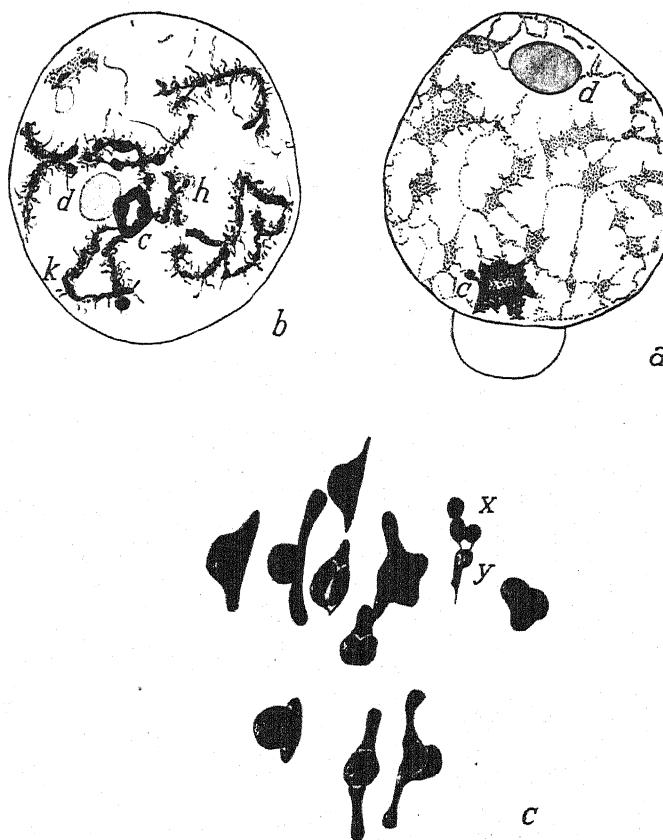


Fig. 12. *Didelphis virginiana* (PAINTER, '24a)—*a* Confused stage showing sex chromosome as chromatin nucleolus (*c*), and true nucleolus (*d*). *b* Early diakinesis. *c* Primary spermatocyte showing X and Y chromosomes.

such interaction apparently does not occur for no crossing over of any kind has been reported for the male. But this is not a universal condition, for in the heterogametic males of fishes crossing over has been observed between the X and Y (WINGE, '22b, '23a; AIDA, '21). Whether this difference between these two forms is related to the fact that the X and Y of *Drosophila* are unequal (fig. 25), while in the fishes the X and Y form an equal pair like all the autosomes (WINGE, '22a), is not clear. If there is some such relation, it would have to be assumed that

the inequality in the XY pair affects also the equal autosome pairs in forms like *Drosophila*, for as already stated, crossing over occurs no more in them than in the sex chromosomes as far as the male is concerned. Nor is there any crossing over in the males of *Drosophila virilis* where the X and Y appear equal.

Still another aspect lies in the possibility that sex determination rests on a number of genes. In the heterogametic sex no free crossing over between such sex genes may then be expected, since it would result in sex intergrades that do not normally occur. Therefore crossing-over between the X and Y could involve only those parts of the chromosomes that do not carry sex genes.

## EXPERIMENTAL WORK ON SEX CHROMOSOMES

Attempts to influence the determination of sex date back to the early periods of history. With the recognition of sex chromosomes a new working basis for such attempts offered itself, for it became evident that any factor that would influence the sex chromosomes would almost certainly have an effect on the development of sex. But apparently no serious endeavor to experimentally affect the sex chromosomes was made until relatively recently. It is true that a great deal of investigation was made in the field of experimentation on gonads and germ cells in general, but MOHR ('19a) was the first to analyze specifically the effects of certain agents (radium and low temperature) on the sex chromosomes. His work was done on the orthopteron *Decticus verrucivorus*, and the results were not decisive. He confirmed the reports of degenerative changes that result in the male germ cells after exposure to radium, but found that in general the sex chromosome shared the detrimental effects observed in the autosomes with no evidence of any selective action by the radium rays. In a few cases however spermatids carrying two X chromosomes (the results of nondisjunction) were observed. The results obtained from the action of subnormal temperatures were in general quite analogous to those from radium although perhaps less intense. On the whole the occurrence of non-disjunction was too rare to justify any conclusion as to the exact influence of the agents employed.

In the following year, SEILER ('20) reported the results of some experimental and cytological investigations of the maturing eggs of *Talaeporia tubulosa*. As in other Lepidoptera the female here represents the heterogametic sex and carries an unpaired or odd X (or Z), while the male has a pair of X (or Z) chromosomes. Theoretically it is chance that decides whether in the heterokinetic division of the egg the X goes out into the polar body or is retained. It was SEILER's endeavor to determine whether the distribution of the X can be affected by external influence, such as high and low temperatures and staleness, and his investigation rested on a study of the heterokinetic divisions of eggs that had been subjected to such treatment. Since the odd X of the female usually lags on the spindle, its movements during this division are open to analysis, and the crucial results may be given in the following table:

	Actual Numbers	On basis of 100 females
Normal (12°—16° C)	61 ♀ : 41 ♂	= 100 ♀ : 84 ♂
Staleness (12°—16° C)	101 ♀ : 146 ♂	= 100 ♀ : 144 ♂
Warmth (30°—37° C)	52 ♀ : 84 ♂	= 100 ♀ : 162 ♂
Cold (3°—8½° C)	49 ♀ : 32 ♂	= 100 ♀ : 65 ♂

(In the above table, retention or expulsion of the X in the heterokinetic division are taken to indicate development of a male or female respectively.)

A large number of figures had to be discarded as indecisive, and it is here that the personal element may enter. But fully granting that errors are possible in the cytological examination of the various lots of material, and further, that the numbers of figures accepted are none too large, there seems no escape from the data as finally given by SEILER: Under normal conditions as well as under subnormal temperatures the X shows a tendency to go out into the polar body, while under high temperatures and in stale eggs the X manifests a tendency to remain in the egg.

The most recent work in this connection has taken the form of an analysis of the effects of ROENTGEN rays on the X chromosomes of *Drosophila*. In a series of short notes MAVOR ('21, '22, '23, '24) has shown that when virgin females of *Drosophila* are subjected to certain doses of ROENTGEN rays, the number of cases of non-disjunction is significantly increased. As BRIDGES ('16) had earlier demonstrated, certain of the exceptional individuals arising from non-disjunctional eggs can be recognized if sex linked factors are introduced into the cross, and it was on that basis that MAVOR computed the effect of the rays. Confirmation of MAVOR's general conclusions came somewhat later from ANDERSON ('24) as the following tables show:

	Total ♀s	% exceptional ♀s	Total ♂s	% exceptional ♂s
MAVOR ('23) . .	3960	0·4	3575	2·3
ANDERSON ('24)	18487	0·4	17225	2·3
MAVOR's Control	12698	0·02	12648	0·06

It is quite plain therefore that the treatment with ROENTGEN rays greatly increases the number of exceptional flies, whose appearance in turn we can only attribute to non-disjunction. That the effect can not be produced on every fly is as true as in case of SEILER's moths, nor is it quite clear what the effect on the autosomes may be. Nevertheless there is here a promising beginning of a new type of investigation of the physiology of the chromosomes.

In this connection reference should also be made to the work of MULLER and DIPPEL ('26). As mentioned elsewhere, L. V. MORGAN ('22) has found females of *Drosophila* in which the two X chromosomes are joined to each other to form a multiple chromosome. She reported that the connection between these X chromosomes is broken on rare occasions. By treating females carrying two joined X chromosomes with ROENTGEN rays MULLER and DIPPEL found that the genetic evidence showed a significant increase in the number of cases of such a breakage of the multiple chromosome.

Finally, it may be said that the amount of crossing over in the sex chromosomes of *Drosophila* may be affected by experimental treatment. But the same thing of course also holds true for the autosomes.

## ORIGIN OF SEX CHROMOSOMES

Our knowledge of the origin and evolution of the sex chromosomes is inevitably dependent on an elucidation of their structure and physiology. As far as our present information goes, it seems evident that basically there is no difference between sex chromosomes and autosomes. This conclusion seems warranted in view of the fact that in the homogametic sex the sex chromosomes behave in every observable way like the autosomes, and also that no exceptional cytological behavior of any chromosomes has been discovered in either sex of a great many, if not the majority of forms, and this despite the fact that in some of them the genetic evidence indicates the presence of sex chromosomes.

Starting with forms of this kind, it is possible to form a series through species in which one sex chromosome of the heterogametic sex grows progressively smaller until those instances are reached in which there is only a single sex chromosome with no trace of a partner. There can be little doubt that such a series expresses the fact that the XO condition was probably derived from a condition in which an equal pair of sex chromosomes was present, and that in fact it is possible that no sex chromosomes (as differentiated from autosomes) were in existence at that time. But beyond a simple statement of this sort such a series can not take us, and its construction throws no light on the processes that brought about the changes in the ancestral chromosomes and converted them to what we know as sex chromosomes.

At the present time we are coming to realize more and more that the phenomenon of sex determination rests on hereditary factors or genes which primarily are not different from the genes that are involved in the development of all other body characters. Moreover, STURTEVANT'S ('21) and BRIDGES' investigations ('22, '25a) have shown that in *Drosophila* at least the genes concerned with sex determination are by no means confined to the sex chromosomes. Evidence such as that gives further support to the hypothesis that the latter type of chromosome does not differ primarily from the ordinary autosome and that its special characteristics are secondary developments.

Such an hypothesis does indeed form the basis for the majority of discussions on the origin of sex chromosomes. Thus STEVENS ('06a) and later WILSON ('11) suggested that the Y chromosome as found in the males of so many species originally resembled the X, and that its present constitution is due to the loss of what might be called the X chromatin. On this basis then, the formula of sex chromosomes for the homogametic female would be XYXY, while for the male it would be XYOY.

A more specific attempt to explain the origin of sex chromosomes on the basis of a loss from one member of a pair has been made by MULLER ('18), who utilizes his observations made in cases of balanced lethals. MULLER had shown that in *Drosophila* a state of heterozygosity with respect to certain genes may be maintained if certain types of lethal genes are also present. Thus an individual may have one pair

of chromosomes showing the following constitution:  $\frac{a \ L}{A \ 1}$  (where a and

**l** are recessive genes that are lethal in the homozygous condition, while **A** and **L** respectively represent their normal allelomorphs). It will be seen that if no crossing over occurs only heterozygous individuals like the parents will be produced since the homozygous offspring always die:

$$\frac{a \ L}{a \ L} = \text{lethal.} \quad \frac{A \ l}{A \ l} = \text{lethal.} \quad \frac{a \ L}{A \ l} = \text{viable and heterozygous.}$$

Such heterozygous individuals look like normal flies since the mutated genes can not appear because they are recessive.

MULLER argued that such a condition would permit the accumulation of changes in one member of a pair of chromosomes that are degenerative in character. Such changes may for instance take the form of inactivation or loss of genes similar to those described under the term deficiency by BRIDGES ('17) and MOHR ('19 b, '23 a, '23 b). Changes of this sort if allowed expression might be decidedly detrimental to the fly, but as recessives they would not appear.

But unless these changes found somatic expression in the males and not in the females (i. e. were sex limited), only one member of a pair of chromosomes could undergo such alteration, and that member is the one that we call the **Y**. If similar degenerations occurred in the **X** such a stock could not be maintained, for in the homogametic sex there would be two **X** chromosomes and the recessives in question would thus be found there in the homozygous condition. This in turn would allow them to appear and if lethal or detrimental the individuals carrying them would be inviable or weeded out by natural selection.

Consideration of this intriguing hypothesis will make it plain that it can not stand without additional assumptions. BRIDGES' work already mentioned has brought out the probability that the loss of a single one of the larger chromosomes produces a lethal effect. If therefore the **Y** is regarded as "empty" of factors or genes, some compensating changes must have taken place during its differentiation from the **X**, and that is of course true also in those cases where the **X** is now unpaired. On the other hand, animals other than *Drosophila* may be so constituted that losses of chromosomal parts are borne with greater impunity.

The question also arises why this process should have occurred in so many forms and nearly always have been confined to one pair of chromosomes. Therefore even if it be granted that the characteristic sex chromosomes originate through the loss or inactivation of certain parts in one member of a pair of chromosomes, it must be realized that we are by no means certain of the way in which such losses have occurred.

## SEX CHROMOSOMES AND SEX DETERMINATION

The bearing of sex chromosomes on sex determination has often been a subject of discussion. In this connection may be mentioned SCHLEIP's excellent essay ('12) which has been followed more recently by the briefer treatments of AGAR ('20), DONCASTER ('20), SHARP ('21) and finally WILSON's review of the whole subject from the cytological standpoint ('25 a). A renewed consideration of the subject must there-

fore seem unnecessary, but in order to round out the present treatment a short account of the various hypotheses wherever they involve sex chromosomes, is given here.

#### A. TROPHO- AND IDIOCHROMATIN

This hypothesis, of which GOLDSCHMIDT ('04) was perhaps the chief proponent, was based on two arguments. The first involves the somewhat non-committal idea that sex determination is correlated in some way with metabolism, and more specifically that unfavorable conditions favor development in the male direction while favorable conditions tend to produce development in the female direction. The second is that every cell contains two kinds of chromatin, idiochromatin which represents the material basis of heredity, and trophochromatin in which rest the metabolic activities of the cell. If we now assume that within certain limits the greater the amount of trophochromatin the more perfect the metabolism, it is only one step further to conclude that fertilized or parthenogenetic eggs equipped with a large amount of trophochromatin will lean toward femaleness in their development, while eggs with a smaller amount of this material will have a development leaning toward maleness. Differences in the amount of trophochromatin could be brought about in several ways. Of these we are concerned only with the one that involves sex chromosomes. These are brought in under the subsidiary hypothesis that the sex chromosomes are composed of trophochromatin. It will readily be seen that differences in their size as well as their presence or absence may on this basis have a very important effect on the process of sex determination.

The hypothesis is primarily weak because it is not supported by sufficiently established facts. Even the basic claim for a dual nature of the chromatin is open to doubt, and although it can not be said that the more general side of the hypothesis has been finally disposed of, GOLDSCHMIDT's own attitude in recent years indicates an abandonment of the more specific points — as for instance his earlier view on the nature of the sex chromosomes.

#### B. HERTWIG'S KARYOPLASMIC RATIO HYPOTHESIS

Although this hypothesis ('05, '06) involves sex chromosomes only somewhat indirectly, its general features should be given in this connection. It will be remembered that R. HERTWIG, chiefly on the basis of his studies on certain protozoa came to the conclusion that the ratio of the nuclear to the cytoplasmic volumes has a definite value under normal conditions for any particular type of cell of a given species.

This value or quotient expressed as  $\frac{K}{p}$  (where  $K$  = nuclear volume and  $p$  = cytoplasmic volume), is subject to change during certain phases of cellular activity, but there is always a tendency to return to the norm. On this basis HERTWIG tried to explain cell division and other phenomena, his ideas about sex determination constituting only a subsidiary part of his general thesis. These ideas are rooted in the observation that in the female gamete or egg the karyoplasmic ratio is altered from

the norm by an increase of the volume of cytoplasm over that of the nucleus, whereas the reverse holds in the mature male gametes or spermatozoa. The gametes are regarded as extreme modifications of the karyoplasmic ratios obtaining in the two sexes, but they nevertheless point to the basic difference between femaleness and maleness; a difference that may be expressed thus: if  $\frac{K}{p} = \text{♀}$ , then  $\frac{K+k}{p} = \text{♂}$ . In a sense then, any factor which can permanently alter the karyoplasmic ratio in an organism is sex determining. It is conceivable that such changes might be brought about after fertilization and cases illustrating such a phenomenon might be sought for instance among protandric hermaphrodites. On the other hand, sex may be determined before fertilization in the egg, and thus in *Dinophilus* the volume of cytoplasm in the female producing eggs is so great that even the addition of the sperm nucleus does not result in a karyoplasmic ratio equivalent to maleness. But in the great majority of cases the period of sex determination is at the time of fertilization itself. The influence wielded by the sex chromosomes is however somewhat indirect as may appear from the following reasoning.

In the protozoa continuous reproduction without conjugation tends toward an increase of the relative amount of cytoplasm (according to HERTWIG). This disturbance in the karyoplasmic ratio can in some cases be rectified by a special growth of the nucleus at the expense of the cytoplasm, during certain stages. The cellular phenomena which occur in the parthenogenesis of higher animals are closely related to such an "autogenous development". Thus in the bee the unfertilized egg after undergoing reduction undergoes a readjustment of this sort, the increase in the volume of the nucleus being such that a ratio equivalent to maleness is produced. In other cases such a compensation is not so readily brought about and there (as in Daphnids and Aphids) parthenogenesis may result in females for several generations. Nevertheless the tendency to increase the nuclear volume over that of the cytoplasm is present there also, and the cumulative effects of several parthenogenetic generations finally bring about a ratio equivalent to maleness.

With these hypotheses in mind, HERTWIG pointed out that if an apyrene sperm (i. e. without chromatin) fertilizes an egg, the development is in a sense parthenogenetic. If as in case of the bee this induces an adjustment of the karyoplasmic ratio, the resulting offspring would tend to be males. On a similar basis, a sperm carrying no sex chromosome is closer to the apyrene condition than a sperm with a sex chromosome, and this in turn causes the consequent development of the fertilized egg to be closer to the parthenogenetic development than would be the case with sperms carrying sex chromosomes. If this parthenogenesis is similar to that of the bee, the tendency to produce males is therewith given. In this sense only are the sex chromosomes regarded as sex producing.

It is unnecessary to point out the multitude of objections to these ideas with which more recent cytological and genetic findings have furnished us. HERTWIG's own disquisition on sex determination in 1912 indicates with great clearness that he himself no longer holds these earlier ideas about sex determination. But it is not so clear that the

more general and basic principles involved in the karyoplasmic ratio may not again play a part in future discussions of the problem here at stake.

### C. QUALITY HYPOTHESIS

A sex chromosome mechanism based on the assumption that there are qualitative differences between the two X chromosomes as they are found for instance in the majority of females was suggested by CASTLE as early as 1903. CASTLE's hypothesis which primarily elaborated the view that sex determination rests on a Mendelian basis, carried with it the idea that both eggs and sperms of a species may be predestined as male or female producing. WILSON ('06) realizing that the sex chromosomes afforded a material basis for this hypothesis considered its possibilities but discarded it within a few years.

The hypothesis rests on the assumption that there is a male producing X and a female producing X chromosome. These may be denoted as  $X^m$  and  $X^f$  respectively. The female carries both types of X, and therefore her sex chromosome formula may be given as  $X^mX^f$ . The female determiner is however always dominant over the male determiner, and since maleness is determined only by  $X^m$  and this is recessive to  $X^f$  it is understandable that males show only one X chromosome. If a Y is present in the male, it may be regarded as a degenerating female determiner which in its existing state is recessive to  $X^m$ . As far as they go these assumptions work out perfectly, but they necessitate the further assumption of a selective fertilization. A sperm carrying  $X^m$  can fertilize only an egg with  $X^f$ , whereas a sperm with a Y or no sex chromosome can fertilize only an egg carrying  $X^m$ . Unless this assumption is made there would be obtained individuals with the formulae  $X^mX^m$ ,  $X^fX^f$  and  $X^f$ , and such individuals do not exist.

No cytological evidence for or against this hypothesis is available. Genetic experiments involving sex linked characters have however furnished evidence that is definitely opposed to the hypothesis, for they make it quite clear that either X of the female may enter into the fertilization nucleus with either type of sperm. In the same way it may be regarded as definitely established that one of the sexes is always homogametic, and therewith the hypothesis must fall.

### D. INDEX HYPOTHESIS

This hypothesis embodies an objection to the view that the sex chromosomes are causally concerned with sex determination. Voiced in several forms by a number of investigators (thus MONTGOMERY '10a, HAECKER, '11, JUNKER, '23) it may be summed up by the statement that chromosomal differences as observed between two sexes of a species are the result and not the cause of sexual differentiation. They are thus merely an index of the activities of deeper lying factors.

Apparent support for this view is to be found in several observations. One of these is on the first spermatocyte division in Aphids and Phylloxera, in which the sex chromosomes apparently always pass to the same pole as the greater mass of the mitochondria. A somewhat similar phenomenon has been described by SOKÓLSKA ('24) in the case

of the first spermatocyte division of *Tegenaria*. Here the two components of the compound X always pass to the same pole and SOKÓLSKA implies that this is also the pole which receives most of the Golgi apparatus. If in such instances as these two the sex chromosome distribution occurs after certain other cell constituents have been distributed and if a correlation obtains between the presence of the latter and that of the sex chromosomes, the indications are that the behavior of sex chromosomes in the division is predetermined. In other words, it is the agency that determines the distribution of the sex chromosomes that is sex determining while they themselves are its outward manifestation.

The argument against such a view may be voiced as follows: If the sex chromosome is merely an index of other phenomena, just as the thermometer is an index of the activities of temperature, then its removal should influence the process of sex determination no more than would a loss of the mercury affect the temperature. But BRIDGES ('16) and several other investigators have shown with great clearness that the removal of an X chromosome has the most profound effect on the sex determination, so that this view can certainly not be maintained.

A different aspect is given to the question if it is admitted that the sex chromosomes are indeed of great immediate importance in sex determination, but that they themselves are controlled by factors of a superior order. Now in an elucidation of the latter, it will appear that they are part and parcel of the basic constitution of the animal. In the case of *Tegenaria* the special distribution of sex chromosomes and Golgi apparatus has been described only in the males and there is every reason to suppose that it does not occur in the females. Therefore it may be assumed that it is the maleness of the basic constitution that is in some way responsible. But since it is admitted that this maleness rests on the fact that the individual in question has an unpaired X chromosome, we are back where we started. An analysis of this whole viewpoint thus shows it to be merely a philosophic exercise.

But it must be admitted that not all cases are as simple as those mentioned. There remain the instances in which a dimorphism in the eggs is present before fertilization and the sex of individuals originating from such eggs is correlated with this dimorphism. Here may be mentioned the well known instances of *Dinophilus*, *Pediculopsis* and perhaps certain of the Seisonida among the Rotifera, where the two types of eggs arise even before the reduction division. The most that can be said in this connection is that sex chromosomes in these cases are not directly involved in the differentiation and that the mechanism involved is not clear as yet.

There remain various cases of hermaphroditism. It is difficult to make a generalization about these, for each one of them presents a separate and individual problem. However all these hermaphrodites have in common the fact that although equipped with the sex chromosomes of one sex, certain characters are evolved that are characteristic of the opposite sex. Thus the hermaphrodites of *Angiostomum nigrovenosum* are basically females but produce sperms as well as eggs. These sperm producing cells primarily contain two X chromosomes like other cells of the hermaphrodite, but in their maturation one X chromosome becomes lost, which is not the case in the maturation of the eggs (BOVERI, '11,

SCHLEIP, '11a & b). In *Icerya purchasi* certain of the germ cells of what is basically a diploid female become haploid, and these give rise to sperms. Germ cells not undergoing this pregametic reduction produce nurse cells and eggs in a perfectly normal manner (HUGHES-SCHRADER, '25, '26). Plainly, in these instances then, the cells of certain regions of the gonad must be subject to some influence that alters their chromosomal constitution. That such a change is possible has been sufficiently demonstrated in connection with experimental work on sex chromosomes and it only remains to analyze the process which is at work in these particular cases. A clue to an explanation is contained in BRIDGES' recent investigation of a gene (minute-n) which has the tendency to bring about a loss of certain chromosomes (BRIDGES, '25a & b).

Slightly different in nature is the case of *Perla marginata* (JUNKER, '23), in which the males contain an ovary-like structure as well as typical testes. This ovary even seems to produce oocytes, but these contain the normal male garniture of chromosomes and not the female garniture of chromosomes (i. e. one unpaired compound X instead of a pair of compound X chromosomes). In an attempted explanation of such a case, it may be pointed out that the sexual characters of a body are not necessarily unalterably fixed. Thus the influence exerted by the chromosomes under normal conditions may conceivably be overridden by other special influences. Thus definitely female characters may appear in individuals carrying the male complement of chromosomes—as in *Thelia* (KORNHAUSER, '19). Here may also be mentioned certain intersexes of *Drosophila simulans* which STURTEVANT ('21) found to contain two X chromosomes like normal females, but in which the mutation of a single gene brought about certain changes in the visible sexual characters. It is granted of course that this represents only a suggestion and that the overriding of the normal chromosomal effect may occur in many different ways. Whatever the nature of the latter may be, they must be instrumental in some way in many cases of hermaphroditism in which no sex chromosomes of any kind can be recognized, and cytological evidence shows both types of sexual products in the hermaphrodite characterized by the same chromosomal garniture.

It is fully realized that these forms represent not only cases of great interest but that they also furnish many obstacles to a final analysis. They are presented here to show that they as well as the relatively more simple cases are consistent with an explanation on a chromosomal basis, and that as long as the latter has not been finally ruled out, cases of this kind do not strengthen the argument for an index hypothesis.

#### E. QUANTITY HYPOTHESIS

Many of the difficulties involved in the foregoing hypotheses are avoided in the hypothesis that each sex chromosome contains a definite (for a given species) quantity of sex determining substance and that it is merely the total amount of the latter that determines the sex of the developing organism. Thus in most cases, if one X chromosome is present the individual becomes a male, while if two X chromosomes are present it becomes a female.

The idea of such a quantitative basis is of course also contained in HERTWIG's karyoplasmic ratio hypothesis and indeed as early as 1903 MORGAN suggested that sex determination in the bee must rest on some such basis. But in its more specific form the hypothesis owes its development chiefly to STEVENS ('05 to '12) and WILSON ('05 to '12). In its simplest form it does not take the Y chromosome into account. WILSON at first suggested that the Y simply represents a less active X chromosome, but later modified this conception to favor the idea advanced by STEVENS ('06a) that the X is merely a Y chromosome with which a definite amount of X chromatin has become associated. The influence of the Y on sex determination was finally regarded as negligible by WILSON, at least in many of the cases (as for instance that of *Metapodius*).

That different quantities of the same substance may bring about the development of two sexes has often been doubted. Nevertheless it is quite possible that the sex determining effect is very similar to that observed in the production of certain somatic characters that appear in different form depending on whether one or two doses of hereditary determiners are present. Again the sex determining substance may partake of the properties of certain enzymes and therefore produce different results depending on the quantity available for reaction.

It will be recognized that here is represented the best of the hypotheses mentioned. Its striking simplicity and the fact that it is applicable to the great majority of known cases in which sex chromosomes have been demonstrated, have caused an almost universal adoption of it. Indeed, the most recent advances in the investigations of sex determination have started from the quantitative hypothesis as a basis in nearly all instances.

#### F. THE ELABORATION OF THE QUANTITY HYPOTHESIS

It was perhaps inevitable that the quantity hypothesis of sex determination in its simplest form should be subject to elaboration and even modification. Progress of this kind owes its inception largely to the older idea that different factors are concerned with the establishment of maleness and femaleness respectively, but that these factors are present in both sexes. An enunciation of such a possibility was made by GOLDSCHMIDT ('11), MORGAN ('11a & b) and WOLTERECK ('11). MORGAN for instance suggested that in cases of male heterogamety a factor for maleness (M) is located in one or more autosomes of all gametes, while the factor for femaleness (F) is present only in the X chromosome. On this basis it is plain that since there are two classes of sperms which differ primarily because of the fact that one carries an X chromosome and the other does not, the sex factors carried by them may be expressed as MF and MO respectively. All mature eggs would be alike and their sex factors would be MF. As a result of fertilization the zygotes MMFF and MMF would be formed, and if it is assumed that MM dominates F, but F dominates M, it becomes possible to express a mechanism of sex determination on these terms. But it must not be forgotten that the formulae merely express the hypothesis that factors for both sexes are present in every individual.

Since 1911 a great part of the further development of this conception is the result of GOLDSCHMIDT's investigations ('12 ff.). These are centered in various attempts to elucidate the origin and nature of intersexual forms among Lepidoptera, and although not bearing directly on the cytological aspects of the sex chromosomes must nevertheless be briefly considered here. GOLDSCHMIDT's conclusions are that in Lepidoptera (where the female is heterogametic) the factors for maleness and femaleness are constant for any one race. If the strength or valence of these factors be expressed numerically, the process of sex determination may be represented as follows:

If  $F = 60$ , and  $M = -40$ ,  
then  $F M$  = female (because femaleness dominates maleness by  
20 units)  
and  $F M M$  = male (because maleness dominates femaleness by  
40 units).

According to GOLDSCHMIDT the sex factors may be conceived of as genes, which partaking of the nature of enzymes incite the production of hormones which in turn direct the development of sex.

GOLDSCHMIDT found however that in crossing certain different races of *Lymantria dispar* with each other, various types of intersexual individuals are produced. The detailed study of such crosses led him to the conclusion that the valence of the sex factors is constant for any one race but may differ from that of other races. Thus if a race in which  $F = 80$  and  $M = -60$  is crossed with a race where  $F = 100$  and  $M = -80$ , certain  $F M$  individuals would be produced in which neither femaleness nor maleness predominate. Such individuals would represent true intersexes, while other types of intersexes might be produced through slight variations in the end result of the actions of the two types of opposed factors. A hint as to the physiology of such a development was given by an analysis of the development of the intersexes. The indications are that these intersexes are individuals that develop as females (or males) up to a certain point, after which development proceeds in the direction of the opposite sex. In normal cases where the cross is intraracial, the valence of the two involved factors is such that one of them maintains the upper hand throughout and the turning point is never reached during the developmental phases, while in the intersexes, the opposing factor causes a change of the sexual development at some point before the end of these phases.

Important as these investigations are, the most interesting point so far as the more limited subject of sex chromosomes is concerned lies in the fact that not only is GOLDSCHMIDT of the opinion that the sex factors are genes that are inherited like true Mendelian genes, but further that the gene or genes for maleness ( $M$ ) are carried in the X chromosome while those for femaleness ( $F$ ) are found either in the cytoplasm of the egg or else the Y chromosome. GOLDSCHMIDT's reasons for favoring the hypothesis that the Y carries the hereditary basis for femaleness are considered elsewhere.

It will be recognized that a more exact genetic analysis of the sex factors could be more easily pursued in a form whose genetic con-

stitution is already better known than is that of any of the Lepidoptera. On this basis an unrivaled object of investigation is the fruit fly *Drosophila*, and the success attending the recent work on the problem of sex in this animal justifies all expectations.

It must not be forgotten that an early approach to such an analysis of the hereditary units accountable for sex determination was made by WILSON in 1911. The phenomena of sexlinked heredity as well as the extreme variation in the size of the X in different species led him to regard this chromosome not as a unit element, but as a compound structure, a hypothesis advanced also by STEVENS ('06 a). Only a limited region of the X was regarded as concerned directly with sex determination—the "sex chromatin", while the rest of the chromosome resembled the autosomes as a carrier of hereditary units.

The first actual recognition of a gene that influences sexual development was however reported by STURTEVANT ('21) in *Drosophila simulans*. It was found that in a certain stock were present many individuals showing a definite type of intersexuality. They were always sterile, but crosses of their apparently normal brothers and sisters to unrelated stocks often produced the same type of intersexuality in some individuals of the  $F_2$  generation (never in  $F_1$ ). Sex ratios of such  $F_2$  generations were approximately  $4 \sigma:3 \varphi:1$  intersex, and suggested, since the normal sex ratio is of course  $4 \sigma:4 \varphi$ , that the intersexes are modified females. This hypothesis was confirmed through the utilization of sex linked genes in further crosses, while the ratios themselves and the fact that the effects were produced only in  $F_2$  generations suggested that a gene is responsible for the modification and that this gene is a recessive. Since  $F_1$  males were never affected it was clear furthermore that the gene in question is autosomal (since males of *Drosophila* have only one X and even a recessive gene carried there should manifest itself). Appropriate crosses involving genes of the second and third chromosome established this as well as the fact that the gene causing intersexuality is in the same chromosome as the gene called plum, that is the second chromosome. Here then was a gene which affected the physiology of the development of sexual characters in such a way that individuals with two X chromosomes and basically females were given the appearance of intersexes.

The recent investigations of BRIDGES ('21, '22, '25 a) have brought out more evidence that the whole phenomenon of sex determination rests on the action of genes and is thus not different basically from the development of any other character of the individual. BRIDGES' work also throws some light on the part taken by the sex chromosomes in this process, and may be explained as follows:

The genetic investigations of *Drosophila* have long made it plain that the development of most if not all characters is dependent on more than one gene. These genes are by no means confined to one chromosome, but a character may depend on genes which are scattered over several chromosomes. Mainly through a chance occurrence of triploid females, individuals were obtained which carried various chromosome combinations. The sex of such individuals may be indicated briefly in the following table, where X = X chromosome and A = one complete (haploid) set of autosomes.

No. of X chroms	Autosomes	Sex
3	2 A	Superfemale
4	4 A	Female
3	3 A	Female
2	2 A	Female
2	3 A	Intersex
1	2 A	Male
1	3 A	Supermale

BRIDGES' interpretation is as follows: The genes that are concerned with sex determination are scattered irregularly over all of the four types of chromosomes as found in *Drosophila*. Roughly speaking, these genes may be classified as female and male determining, and the two types are in a sense opposed to each other. It so happens that in the X the genes for femaleness preponderate over those for maleness, so that taken as a whole this chromosome is female determining. The second and third chromosomes however have this condition reversed and in them the male determining genes preponderate over the female determining genes. The status of the tiny fourth chromosome is still uncertain but nevertheless it is evident that taken as a group the autosomes are male determining. It thus appears that sex determination is a question of what BRIDGES terms "genic balance", and it rests in effect on the ratio between the number of X chromosomes and the number of sets of autosomes. Indeed, very similar conclusions have been voiced by SCHWEITZER ('23) and v. WETTSTEIN ('24) as a result of their investigations of the sex conditions in mosses.

The evidence is thus quite strong that as a carrier of genes the X chromosome differs in no essential way from the autosomal chromosomes. Indeed, on this basis, sex determination itself loses the special position which it has always occupied in the minds of most investigators, for it now becomes a process regulated by hereditary genes like any other development of the body. If this view is recognized a good many difficulties of the old problem are removed. Thus there may be mentioned the hitherto contradictory evidence contained in the fact that in a few groups (Lepidoptera and Aves) the female instead of the male is heterogametic. Instead of considering that 2 X is equivalent to femaleness and 1 X to maleness (with these relations unaccountably reversed in the two groups mentioned), it must be recognized on the above basis that the so called sex chromosomes are by no means the only chromosomes concerned with sex determination. If then the sex genes are scattered irregularly over autosomes as well as the X, it may well be that the sex genes in the X of Lepidoptera happen to be preponderately male determining while the autosomes are female determining (i. e. the reverse condition to that of *Drosophila*), and sex determination is then just what might be expected. At any rate, the peculiar contradiction resting in the explanation based on the simplest form of the quantity hypothesis therewith loses its substance.

Also, it need hardly be pointed out that this most recent conception of the mechanism of sex determination is in no way to be regarded as inimical to the hypothesis that in some animals at least,

the final expression of sex is brought about through the instrumentality of hormones. In what way the hormones depend on the genes is of course still an open question, but the idea of a genetic basis is not affected by physiological interpretations of its action. Again, there seems to be no reason to suppose that the effects of genes involved in sex determination differ from the effects produced by other genes in being immune to environmental agencies. It is therefore no argument against the genetic hypothesis to point out that an organism of one sex may through environmental means be induced to show the phenotype of the opposite sex. The nature of such a change is basically equivalent to that which occurs in certain plants which under the influence of abnormally high temperatures produce white flowers although they are genotypically redflowered.

If the problem of sex determination rests on the same basis as any other phenomenon of heredity, its solution becomes detached from the analysis of those special cytological characters that distinguish the sex chromosomes from the autosomes. It must be admitted that therewith a source of confusion would be eliminated and a considerable advance made toward a clearer definition of the issues involved.

## THE Y CHROMOSOME AS A CARRIER OF GENES

The exact nature of the Y chromosome has long been a matter of speculation. In 1909 Castle suggested that it may be a carrier of the factors for the secondary sexual characters of the heterogametic sex, but this hypothesis was not subjected to an actual test by him. Certainly it was quickly discovered that such an explanation is not applicable to all cases, for WILSON found ('07b, '09b, '10a) that in *Metapodius*, males lacking a Y chromosome appeared normal in every respect. Indeed, the many instances in which the X is normally without a partner in the heterogametic sex were sufficient evidence for the fact that the Y is not always a necessary constituent of the chromosome complex.

WILSON showed that starting with types in which the Y is morphologically indistinguishable from the X, a series of species may be listed showing a gradual dwindling of the Y and culminating in its complete disappearance. It needs not be pointed out that such a series does not necessarily depict the history of the Y, but it nevertheless serves to emphasize the probability that in general it is a degenerating chromosome doomed to disappear in many cases.

The well known studies on sex linkage in *Drosophila*, culminating in BRIDGES' work on non-disjunction ('16) served to strengthen the idea that the Y is more or less negligible as a carrier of the factors of heredity. The fact that individuals with the sex chromosome constitution XXY are normal females and XO individuals are normal males to all outward appearance, seemed to demonstrate that fact very clearly. But it must not be forgotten that BRIDGES himself discovered that XO males are sterile and that therefore the Y must have a most important part in the maintenance of the species. Nevertheless the first recognition and exact location of a gene in the Y of *Drosophila melanogaster* was

not made until very recently (STERN, '26a, '27) so that every indication points to the fact that in *Drosophila* the Y carries very few genes.

In frogs the presence or absence of a Y was long in doubt. However WITSCHI's breeding experiments led him to suggest as early as 1914 that in these animals the male has a Y and that in this is carried a factor for maleness, a suggestion to which his more recent work lends support.

Evidence that the Y (or the W in Lepidoptera) may be of the utmost importance in sex determination, has recently been advanced by GOLDSCHMIDT in the case of *Lymantria dispar*. It will be remembered that in the Lepidoptera the females are heterogametic. As has been explained elsewhere, GOLDSCHMIDT's investigations of intersexuality have led him to the conclusion that the factors for femaleness (F) and maleness (M) have a very definite valence for any one race of *Lymantria*, but that this valency may differ from that obtaining in other races. GOLDSCHMIDT also arrived at the conclusion that F is transmitted only through the female and that such transmission must occur either through the cytoplasm of the egg or the W chromosome. At first inclined to favor the former alternative, he was later ('19, '20, '22) led to advocate that it is the W that carries F. His reasons may be briefly given as follows:

According to GOLDSCHMIDT, in any one race  $F > M$ , but  $MM > F$ . Females may be designated as  $F M m$  (where m merely denotes the absence of the factor for maleness in the W chromosome), and males as  $F M M$ . In another race "s", the valences are higher and thus  $M_s > F$ . An actual cross of the two races would appear as follows:

$$\begin{array}{cccc} \text{♀} & \text{♂} & \text{♂} & \text{♂} \\ F M m \times F_s M_s M_s = & F M M_s + F M_s m. \\ (\text{The } F_s \text{ of the } \text{♂} \text{ parent not being transmitted.}) \end{array}$$

In other words, all offspring of the cross should be males. However, in a few instances such crosses also gave rise to a few females. On breeding such females, GOLDSCHMIDT found that they carried the factor  $F_s$  which could have come only from the father. Since this factor can be carried only in the cytoplasm of the egg or else the W chromosome, only one conclusion seems possible. Egg cytoplasm can not be transmitted through the male and therefore the male here in question must have carried a W chromosome—acquired perhaps through non-disjunction.

FEDERLEY ('22) was also inclined to believe that the W carries something that pertains to the development of femaleness. One difficulty however remains. If the factor for femaleness is carried in the W, then half of the eggs after reduction do not carry it. Nevertheless the factor for femaleness is effective in both sexes. GOLDSCHMIDT ('22) therefore suggested that this factor, located in the W chromosome, impresses its effect on the cytoplasm of every egg before the reduction division. Its influence therefore remains even in eggs which have eliminated the W chromosome. It will be apparent that further work in this connection is called for and that GOLDSCHMIDT's evidence is incomplete.

Finally mention should be made of other cases in which the Y carries genes. SCHOFIELD ('21) and CASTLE ('21) gave some evidence

that the gene for "webbed toes" in man is carried in the Y, and very convincing conclusions for regarding the Y as a carrier of genes were adduced by de ZULUETA ('25) in the beetle *Phytodecta*. The best cases have been reported however in the fishes. SCHMIDT ('20) found that in *Lebistes reticulatus* the factor for a small black spot on the dorsal fin was transmitted only through the males for five generations. The natural conclusion that the Y chromosome of the male carries the gene in question was confirmed by WINGE ('22b) who also found several other genes in that chromosome, as did AIDA ('21) in *Aplocheilus latipes*.

The evidence is thus clear enough that the Y chromosome is by no means always negligible as far as heredity is concerned. It is to be hoped that the discovery in it of genes and therewith opening it to genetic analysis will throw light on those processes that have caused its disappearance or degeneration in so many instances.

## PARTHENOGENESIS

### DIPLOID PARTHENOGENESIS

If parthenogenetic development of an egg occurs with the full or diploid number of chromosomes—whether this number be restored in some way after a typical reduction division or whether the latter be entirely omitted—the individual developed is in the great majority of cases a female. This of course is just what might be expected if the chromosomes of the offspring duplicate those of a female parent. Little else need be said of this subject as a whole, and the more specialized problems do not fall under the present discussion.

### HAPLOID PARTHENOGENESIS

Although diploid parthenogenesis thus falls in very naturally with the chromosomal and genetic hypothesis of sex determination, a great deal more of difficulty is encountered in the case of those individuals which develop with the reduced or haploid number of chromosomes. In the first or original form of the quantity hypothesis in which the amount of X chromatin was regarded as the material basis of sex determination, a ready explanation was available for the fact that among animals all haploid individuals appear to belong to the male sex. It was held simply that 1 X chromosome determined the male condition and 2 X chromosomes determined the female condition, regardless of the autosomes that might also be present. But it has already been pointed out that all recent evidence indicates that the autosomes are by no means thus to be ignored and that sex in most animals is in effect dependent on the ratio between the chromosomes which have a net male determining tendency and those which have a net female determining tendency. Triploid and tetraploid individuals in which the same ratio obtains as in the diploid individuals should therefore be of the same sex as is the latter, and the same rule should hold also in regard to haploid individuals. The cor-

rectness of the hypothesis in case of polyploid *Drosophilas* has already been demonstrated by BRIDGES ('21, '22, '25 a), who has also adduced some evidence that in these Diptera at least, haploid individuals would be females if they were viable ('25 b, '25 c).

What then is to be done with the cases of *Trialeurodes* (SCHRADER, '20, THOMSEN, '25), *Tetranychus* (SCHRADER, '23 b), and *Icerya* (SCHRADER & HUGHES-SCHRADER, '26), in which the cytological and breeding data clearly indicate that males always develop from reduced eggs and develop with the haploid number of chromosomes? To these cases must be added similar observations in many Hymenoptera in which the cytological evidence is on the whole less decisive because of certain complicating factors. In regard to the last named group, doubt has often been expressed about the haploid state of the males and BÖRNER ('25) has recently questioned the evidence in the other cases as well. It can only be said that one familiar with the cytology of these forms can not brush them aside so easily with such a blanket denial.

It has been suggested (SCHRADER & STURTEVANT, '23) that a compromise may be brought about in the following way: If we arbitrarily call maleness the plus, and femaleness the minus direction and let  $X = -6$ , and  $A$  (a set of autosomes)  $= 2$ , then we can regard the effective relation in sex determination as the algebraic sum of these two types of chromosomes. Some of the individuals obtained by BRIDGES would give the following values:

$$\begin{aligned} \text{Female: } & 2 X + 2 A = -8 \\ \text{Intersex: } & 2 X + 3 A = -6 \\ \text{Haploid: } & X + A = -4 \\ \text{Male: } & X + 2 A = -2. \end{aligned}$$

If it is supposed that the threshold value for maleness is at  $-5$ , and for femaleness at  $-7$ , it would be clear that haploid individuals would be males just as they are in *Tetranychus*. But as has been said, BRIDGES' evidence indicates that haploid *Drosophilas* would not be males, but females. Evidently therefore, cases in which haploid individuals are males are not to be put on the same basis (as far as sex determination is concerned) as *Drosophila* and probably most other forms.

Indeed, basic differences in this regard are indicated also in other ways. In all animals of the *Drosophila* type, individuals with only the haploid number of chromosomes are not viable, and in *Drosophila* itself the loss of any one chromosome of the diploid set (except the  $X$  and the tiny fourth chromosome) apparently is lethal. Again, in plants like *Datura* in which viable haploid individuals have been obtained, the reproduction of the latter is subject to irregularities because the distribution of the chromosomes in the reduction division results in abnormal combinations. It is therefore not unfair to suppose that forms in which haploidy occurs normally have undergone certain preparatory modifications. These not only brought about viability of individuals in the haploid state but also resulted in a regulation of the reduction division (*Pseudococcus* may represent an animal in which such modifications may be in progress).

But how such processes affected sex determination is still an obscure point. It is possible that in forms with haploid males the old

quantity hypothesis or the algebraic sum hypothesis represent an explanation, but it must be admitted that that is not likely. It has been suggested by GOLDSCHMIDT ('20b) that factors for maleness (MM) might be carried in or their effect impressed on the cytoplasm of the egg, and that these factors are constant. If each X chromosome then carries a factor for femaleness (F) and  $FF > MM > F$ , then the development of maleness or femaleness is in a sense determined by the presence of one X (as in haploidy) or two X (as in diploidy) respectively. Nothing but further researches can throw light on this old and mooted question as well as determine whether these animals have sex chromosomes as they are ordinarily conceived of.

## SYSTEMATIC REVIEW OF SEX CHROMOSOMES

In considering sex chromosomes as they occur in different forms of animals and plants, emphasis is here laid on those cases which present exceptional features. The tables appended to the discussions of the different groups however cover the ground as completely as possible, orthodox cases being given as impartially as those with special points of interest.

As far as is feasible only cytological evidence is considered in the tables. Lists and tables of the results of chromosome investigations as published by previous reviewers have been of great help, and this is especially true of those of E. B. HARVEY ('16, '20). However I have not followed Mrs. HARVEY in tabulating all the varying conclusions in those instances where several investigators have reported on one and the same species. Instead I have given only those findings which to me seemed most trustworthy, taking care however to draw attention to the cases in which a decision was not possible. In any case, a complete list of references is always given in the appropriate column, so that even those papers the conclusions in which I have not accepted can easily be consulted. Like tabulators before me, I have undoubtedly made errors, omissions and misinterpretations. No doubt the fault for most of these must rest on my own shoulders, although I can not refrain from pointing out that in not a few instances the original papers are guilty of ambiguity and self contradiction.

Taxonomy has been considered as secondary to cytology in this systematic review, and wherever the volume of investigations and the character of the findings have called for it I have not hesitated to sum up the work under the order and even separate families, while in other groups it has been deemed unnecessary to go beyond the phylum.

Finally I would like to emphasize once more that the name "heterochromosome" is applicable to any chromosome that is distinguishable from ordinary chromosomes by certain peculiarities of behavior. The "sex chromosome" is therefore a special form of heterochromosome and since the latter is a much more inclusive term, the two are not synonymous.

It has been found unavoidable to use a system of abbreviations in the tables. Their explanation follows:

## ABREVIATIONS NOT SELF EXPLANATORY

approx.	= approximately,
clv.	= cleavage,
degen.	= degenerate,
m.	= microchromosomes,
macro:	= macrochromosomes, used by PAINTER for larger chromosomes of reptiles,
micro.	= microchromosomes, used by PAINTER for smaller chromosomes of reptiles,
oog.	= oogonia,
parth.	= parthenogenesis,
s.	= supernumerary chromosome,
spg.	= spermatogonia,
tid	= spermatid or ootid,
XY	= XY pair (only in columns tabulating meiotic behavior), with members fused,
X + Y	= XY pair (only in columns tabulating meiotic behavior), with members separated,
X <sup>I</sup> X <sup>II</sup> etc	= Compound X (only in columns tabulating meiotic behavior), with members fused,
X <sup>I</sup> + X <sup>II</sup> etc	= Compound X (only in columns tabulating meiotic behavior), with members separated.

Numbers given under the captions "1st cyte" and "2nd cyte" appertain to the chromosomes as they are found in the metaphases of the two maturation divisions.

## PLATYHELMINTHES

The great majority of forms found in this phylum is hermaphroditic. Cytological investigations of such types have brought to light some interesting conditions, but there appears to be no definite record of an occurrence of sex chromosomes.

Chromosomes of this character have however been described in one of the dioecious Trematoda, *Schistosomum (Bilharzia) haemotobium*, by LINDNER ('14). LINDNER did not have sufficient material to make a fully conclusive analysis of the case, but in general the following conclusions seem warranted:

There are 14 chromosomes in the spermatogonia. Metaphases of the first spermatocyte division show 6 tetrads grouped as a circle with 2 smaller chromosomes in the middle. The 6 tetrads divide normally, but the 2 smaller chromosomes pass undivided to one pole. The second spermatocytes thus carry 6 and 8 chromosomes respectively, and since all the chromosomes divide in the second division, there are two types of sperms. LINDNER's material did not enable him to give an account of the oogenesis nor is even a count of the chromosomes in the female available. Nevertheless it seems probable that the 2 small chromosomes which in the male fail to divide in the first division, represent a compound X. Since this appears to have no partner, the female probably would have 2 more chromosomes than the male in as much as it may be expected to carry 2 compound X chromosomes.

## PLATYHELMINTHES

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless, otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Schistosomum</i> <i>(Bilharzia)</i> <i>haematobium</i>	14 spg.	8	6 8	6 8	Probably an un- paired $X^I + X^{II}$ in male	LINDNER '14

## NEMATELMINTHES

In only one of the classes of this phylum, the *Nematoda*, have sex chromosomes been described. Here there are found cases that illustrate with schematic simplicity the mechanism through which a chromosomal dimorphism is brought about in the two sexes. Of these the best known example is *Ancyraanthus cystidicola* (MULSOW, '11, '12) the female of which shows 10 autosomes and 2 X in the diploid condition whereas in the male there are 10 autosomes and only 1 X. The pronuclei of all eggs carry 5 autosomes and 1 X, and the sperms are of two kinds — 5 autosomes and 1 X, and 5 autosomes with no sex chromosome. Fertilization then restores the diploid number, the type of sperm determining whether the egg develops with 11 or 12 chromosomes and becomes a male or a female respectively. The clearness with which all the processes of maturation and fertilization can be demonstrated in this worm and the fact that the chromosomes are recognizable at nearly all of the crucial stages have made it a stock example in many general treatises. In addition to *Ancyraanthus* there are several other Nematodes which although presenting greater difficulties from the technical standpoint, are basically just as simple.

More rare are the cases which parallel the conditions just mentioned except for the fact that the X is represented by more than one chromosome, i. e. is compound in nature. Here may be mentioned *Ascaris lumbricoides* (EDWARDS, '10b; WALTON, '24) in which the male's diploid set of chromosomes includes 38 autosomes and a compound X of 5 elements — a total of 43 chromosomes. All female pronuclei carry 24 chromosomes, that is probably 19 autosomes and 5 X elements, while the sperm nuclei may carry either 19 autosomes and no sex chromosomes, or else 19 autosomes and a compound X of 5 elements. As a result, two types of embryos are formed,  $38 + 5$  X elements and  $38 + 10$  X elements, which develop into males and females respectively.

In still another group of cases there is found a superficial resemblance to the types already considered. They are however complicated in several ways and a final analysis of such special features is still outstanding. The greatest and perhaps most frequent difficulty arises from the fact that the chromosomes as seen in the germ cells are of a character different from those found in the soma. The number of chro-

mosomes in somatic cells is in these cases larger than the number in the germ cells (usually the former is a multiple of the latter), and two main explanations are open for this condition. One of these assumes that the chromosomes as seen in the germ cells are unit elements, but that they undergo a process of fragmentation in the soma; the other regards the somatic chromosomes as unit elements which undergo a definite type of fusion in the germ cells so as to form a certain number of multiple or "Sammel" chromosomes. AGAR ('20) advocates the former interpretation while WALTON ('24) favors the latter, although he admits that fragmentation may play an additional part in some cases. It must be conceded that several of the worms studied by WALTON strongly support his contentions, even though a final conclusion in regard to the Querkerbe as an indication of fusion may be deferred.

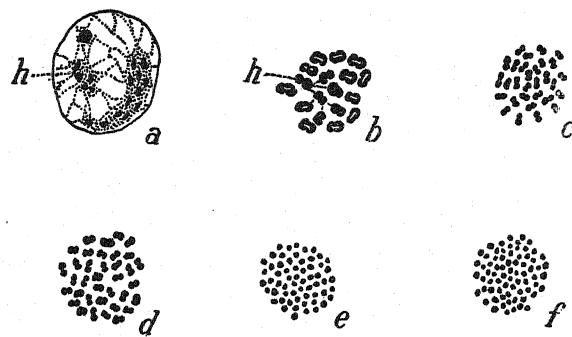


Fig. 13. *Toxascaris canis* (WALTON, '24)—*a* Prophase of first spermatocyte showing sex chromosomes (*h*) separated from autosomal mass. *b* Metaphase of first spermatocyte showing twelve autosomal "ditetrads" and six sex chromosome "tetrads". *c* Fertilization nucleus with 30 dyad chromosomes (male number). *d* Fertilization nucleus with 36 dyad chromosomes (female number). *e* Somatic metaphase of male, showing 60 monads. *f* Somatic metaphase of female, showing 72 monads.

A simple type of the preceding group is *Acuaria spiralis*, in which each sex chromosome as well as each autosome as it is found in the germ cells, gives rise to two elements in the soma. But whereas there is only a single X in the germ cells of the male of this species, another species — *Toxascaris canis* — has a compound X of 6 elements (fig. 13). Each of these gives rise to two chromosomes in the soma. This last case therefore presents the double complication of compound as well as multiple chromosomes, and it is only one of several that show such a condition (WALTON, '24).

Further difficulties are encountered in those cases where the X is associated more or less intimately with an autosome. Thus, WALTON ('24) described in the germ cells of *Physaloptera turgida* an X which is always accompanied by an autosome in its various movements, although no visible bond exists. Again, BOVERI suggested that the XY pair described by EDWARDS ('11) in *Ascaris felis* (*Belascaris mystax*) in reality represents an autosomal tetrad to which an X has become attached. WALTON ('21, '24) was inclined to BOVERI's view and be-

lieved that while the autosomal tetrad divides normally in both divisions, the X divides only in the second. Thus while all sperms carry 9 chromosomes, one of the chromosomes included in half the sperms is a multiple and represents an autosome fused with an X.

This brings us to the case of *Ascaris megalocephala* with its two varieties, *univalens* and *bivalens*, that are characterized by the diploid chromosome numbers 2 and 4 respectively. Normally, the chromosomes seem to be alike in the two sexes. But in either sex there are now and then found individuals which show a chromosome number in the germ cells which is higher than normal. As early as 1895 HERLA described an extra chromosome of small dimensions in a specimen of *Ascaris megalocephala bivalens*, and suggested that this might have had its origin in a fragmentation of the normal chromosomes, or that the individual in question had arisen from a dispermic egg (i. e. fertilized by a sperm of *bivalens* and a sperm of *univalens*). BORING ('11) later pointed out that the last named explanation was not tenable in HERLA's case, since the extra chromosome was considerably smaller than a normal chromosome of either variety. BOVERI ('99) described several individuals of *univalens* showing 3 chromosomes and attributed them to eggs which had not eliminated one of the normal 2 chromosomes in the maturation. As far as BOVERI's cases are concerned, this explanation was probably correct, for his figures show all 3 chromosomes to be of the same size. In 1909 however, Miss BORING showed an extra chromosome of smaller size in a *bivalens*. BOVERI believed this extra chromosome to be an X chromosome which is normally fused with an autosome but was here accidentally detached. EDWARDS ('10a, '10b) supported BOVERI in this hypothesis and FROLLOWA ('12) claimed that whereas only one detached X is ever found in such exceptional males, females of this type always show 2 X. On this basis then, normal cases of *Ascaris megalocephala* have sex chromosomes, but these are ordinarily fused with the autosomes in such manner as to defy detection. In the males only 1 X is thus present, while the homogametic females carry 2 X.

The problem was attacked in another way by GUIEYSSSE-PELLISSIER ('09), KAUTZSCH ('13), GEINITZ ('15), and WALTON ('24). As is well known, the chromosomes of the germ cells of *Ascaris megalocephala* are multiple in nature and in the soma cells break up into their components. If therefore the female has 1 X more than the male, that fact, so difficult to demonstrate by measurements, may appear in the number of chromosomes that appear in the soma. GUIEYSSSE-PELLISSIER found indeed that different embryos of *bivalens* showed either about 62 or else 70 chromosomes. Assuming that these two types represent male and female respectively, the X as found in the germ cells is thus composed of 8 elements. KAUTZSCH, basing his conclusions on work done on *univalens* did not agree with GUIEYSSSE-PELLISSIER and estimated that the chromosome numbers of *bivalens* should be 135 and 144. WALTON ('24) and several other investigators pointed out however that the individual chromosomes of the two varieties are not equivalent and that computations based on studies of *univalens* can not be applied to *bivalens*. The number of chromosomes given for *bivalens* by WALTON himself was 96 and 104.

In his investigation of *univalens* KAUTZSCH utilized some aberrant embryos which contained only the paternal chromosome in their cells. The numbers arrived at were 63 and 72. GEINITZ ('15) and WALTON ('24) however found the numbers to be 52 and 60.

In view of the discrepancies in the total number of chromosomes reported by the various observers, it seems peculiar that so close an agreement should obtain in regard to the number of chromosomes in the soma by which the two sexes differ. It is of course possible that the chromosomes of the germ cells may differ in respect to the degree to which they break up in the somatic cells of different individuals. Such variation can not be shared by the sex chromosomes however for all observers agree that they always give rise to 8 or 9 elements. All in all it is perhaps safe to say only that there are strong indications that the male of *Ascaris megalcephala* represents the XO, and the female the XX condition.

With one exception, no cases of an XY condition have been definitely established in the phylum. The exception in question is *Contracaecum incurvum* (*Ascaris incurva*) in which GOODRICH ('14, '16) described a compound X of 8 elements and a large Y for the male. The female probably has 2 compound X chromosomes of 16 elements. As already mentioned, *Ascaris felis* (*Belascaris mystax*) may also have an XY in the male, although both BOVERI and WALTON opposed such an interpretation. MARCUS ('06) reported an XY in the males of a form that he called *Ascaris canis*, but WALTON believed that MARCUS studied *Belascaris triquetra* and that there is no Y but a compound X of 2 components in that species.

Some mention should be made of *Rhabditis aberrans*, in the males of which KRÜGER ('13) described 2 heterochromosomes. These divide equationally in the first, but go to opposite poles in the second spermatocyte division. Only one of them is finally included in the developing sperms, the other being lost. It is possible that the latter may be a Y, although Fr. KRÜGER herself took both heterochromosomes to be X chromosomes. A Y may possibly be also involved in the case of *Angiostomum* (SCHLEIP, '11, BOVERI, '11) where the male germ cells of the hermaphroditic generation contain 2 heterochromosomes as well as the female germ cells. It is significant however that in the meiosis of the male cells the 2 heterochromosomes show heteropycnosis while this does not occur in the female germ cells. The suggestion that one of the X chromosomes as found in the female cells is transformed into a Y in the male cells is therefore not an impossible one, especially as it seems safe to assume that the hermaphrodite is basically a female. The loss of one of the heterochromosomes in the second spermatocyte division occurs just as it does in *Rhabditis aberrans*, and it would be the Y that one might expect to be thus eliminated in the present instance. It is evident that no final conclusion is possible at the present time.

Further study of the complications that are so commonly encountered in this phylum may throw a good deal of light on the question of compound sex chromosomes. It is also to be hoped that further investigations of such features as diminution, hermaphroditism and complicated life cycles may be made in this interesting group.

## NEMATODA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Acuaria spiralis</i>	12 ♀ soma 11 ♂ soma	6 ♀ 5 + X	6 ♀ 5 5 + X	6 ♀ 5 5 + X	Each chromosome has 2 components	WALTON '24
<i>Ancyracanthus cystidicola</i>	12 oog. 11 spg. 11 & 12 clv.	6 ♀ 6 6	6 ♀ 5 6	6 ♀ 5 6	—	MULSOW '11, '12
<i>Angiostomum (Rhabditis) nigrovenosa</i> bisexual generation	11 & 12 clv.	6 ♀ 6	6 ♀ 5 + X 5	6 ♀ 5 + X 5	Sperms with 5 probably degenerate	SCHLEIP '11a, 11b BOVERI '11
hermaphroditic generation	12 oog. 12 ♀ soma	6 ♀ 7 (= 5 + 2 sex chroms.)	6 ♀ 7	6 ♀ 5 6	One sex chromosome is lost in one of every two tids	
<i>Ascaris incurva (Contracaecum incurvum)</i>	35 spg.	13 + X <sup>I</sup> Y + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> + X <sup>VI</sup> + X <sup>VII</sup> + X <sup>VIII</sup> 21 ♀	13 + Y 13 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> + X <sup>VI</sup> + X <sup>VII</sup> + X <sup>VIII</sup> 21 ♀	—	—	GOODRICH '14, '16
<i>Ascaris lumbricooides</i>	43 or 48 clv.	19 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> 24 ♀	19 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> 24 ♀	—	2nd cyte division equational	EDWARDS '10a, '10b BONNEVIE '02 WALTON '24
<i>Ascaris megalocephala</i> var. <i>univalens</i>	52-63 ♂ soma 60-72 ♀ soma	1 1 ♀	1 1 ♀	1 1 ♀	Germ cell chromosomes multiple. Autosomes forming multiple with X. X = 8 or 9 components	BOVERI '11 EDWARDS '10a, '10b KAUTZSCH '13 GEINITZ '15 WALTON '24
<i>Ascaris megalocephala</i> var. <i>bivalens</i>	62-135 ♂ soma 70-144 ♀ soma	2 2 ♀	2 2 ♀	2 2 ♀	Germ cell chromosomes multiple. Autosomes forming multiple with X. X = 8 or 9 components	BORING '11 GUIEYSSÉ PELLISSIER '09 KAUTZSCH '13 FROLOWA '12 WALTON '24
<i>Belascaris mystax</i> ( <i>Ascaris felis</i> )	18 ♂ soma 18 ♀ soma	8 + XY 9 ♀	8 + X 8 + Y	8 + X 8 + Y	Possibly no XY but X attached to autosome	EDWARDS '11 WALTON '16, '21, '24
<i>Belascaris triquetra</i> ( <i>Ascaris canis</i> of MARCUS?)	44 or 48 clv.	10 + X <sup>I</sup> + X <sup>II</sup> 12 ♀	10 + X <sup>I</sup> + X <sup>II</sup> 10 12 ♀	10 + X <sup>I</sup> + X <sup>II</sup> 10 12 ♀	Germ cell chromosomes are multiple	MARCUS '06 WALTON '24

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Contracaecum spiculigerum</i>	15 spg. 16 oog.	8 8 ♀	7 8 8 ♀	7 8 8 ♀	—	WALTON '24
<i>Cruzia tentaculata</i>	12 spg.	5 + X 6 ♀	5 5 + X 6 ♀	5 5 + X 6 ♀	Germ cell chromosomes are multiple	WALTON '24
<i>Filaria papillosea</i>	11 or 12 clv.	6 ♀	6 ♀	5 5 + X	—	MEVES '15
<i>Ganguleterakis spinosa</i>	20 ♂ soma 24 ♀ soma	4 + X <sup>I</sup> + X <sup>II</sup> 6 ♀	4 + X <sup>I</sup> + X <sup>II</sup> 4 6 ♀	4 + X <sup>I</sup> + X <sup>II</sup> 4 6 ♀	Germ cell chromosomes are multiple	WALTON '24
<i>Heterakis dispar</i>	9 spg. 10 oog.	4 + X 5 ♀	4 4 + X 5 ♀	4 4 + X 5 ♀	—	GULICK '11
<i>Heterakis inflexa</i>	—	4 + X 5 ♀	4 4 + X	—	—	GULICK '11
<i>Heterakis papillosa</i>	18 spg. 20 oog.	4 + X 5 ♀	4 4 + X 5 ♀	4 4 + X 5 ♀	—	WALTON '24
<i>Heterakis vesicularis</i>	9 spg. 10 oog.	4 + X 5 ♀	4 4 + X 5 ♀	4 4 + X 5 ♀	—	GULICK '11
<i>Heterakis</i> sp.	9 spg.	4 + X 5 ♀	4 4 + X 5 ♀	4 4 + X 5 ♀	—	BOVERI '09
<i>Nematospira turgida</i>	11 spg. 12 oog.	5 + X 6 ♂	5 5 + X 6 ♀	5 5 + X 6 ♀	Germ cell chromosomes are multiple	WALTON '24
<i>Physaloptera turgida</i>	10 oog.	5 5 ♀	4 4 + X 5 ♀	4 4 + X 5 ♀	Germ cell chromosomes are multiple	WALTON '24
<i>Protospira muris</i>	—	4 + X 5 ♀	4 4 + X 5 ♀	4 4 + X 5 ♀	—	WALTON '24
<i>Rhabditis aberrans</i>	18 clv.	10 18 ♀	10	9 18 ♀	Probably all sperms degener- ate. No re- duction in egg (parth.)	KRÜGER '13
<i>Rhabditis pellio</i> (SCHNEIDER)	—	6 + X 7 ♀	6 6 + X 7 ♀	—	X in male to pole in 1st or 2nd	KRÖNING '23
<i>Rhabditis</i> sp.	—	6 + X 7 ♀	6 6 + X 7 ♀	7 ♀	X of male to pole in 1st or 2nd	KRÖNING '23

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Sclerostomum edentatum</i> (and other <i>Sclerostomum</i> species of horse)	11 spg. 12 oog.	5 + X 6 ♀	5 5 + X 6 ♀	6 ♀	X of male to pole in 1st or 2nd	KÜHTZ '13
<i>Strongylus filaria</i>	11 spg.	5 + X 6 ♀	5 5 + X 6 ♀	5 5 + X 6 ♀	—	KRÖNING '23 STRUCKMANN '05
<i>Strongylus paradoxus</i>	12 oog. 11 spg. 11&12 clv.	5 + X 6 ♀	5 5 + X 6 ♀	5 5 + X 6 ♀	—	GULICK '11 KRÖNING '23
<i>Strongylus micrurus</i>	—	5 + X 6 ♀	5 5 + X 6 ♀	5 5 + X 6 ♀	—	KRÖNING '23
<i>Strongylus tenuis</i>	—	5 + X 6 ♀	5 5 + X	5 5 + X	—	GULICK '11
<i>Syphacia obvelata</i>	15 spg. 16 oog.	7 + X 8 ♀	7 7 + X 8 ♀	7 7 + X 8 ♀	—	WALTON '24
<i>Toxascaris canis</i> ( <i>Ascaris</i> )	30 spg. 36 oog. 30 & 36 clv.	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> + X <sup>VI</sup> 18 ♀	12 12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> + X <sup>VI</sup> 18 ♀	12 X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> + X <sup>VI</sup> 18 ♀	—	WALTON '16, '18, '24
<i>Trichosomoides cressicauda</i>	8 oog.	4 4 ♀	3 4 4 ♀	3 4 4 ♀	—	WALTON '24

## MOLLUSCA

Among Mollusca heterochromosomes of any kind seem to have been reported only in several orders of the Gastropoda. The many earlier investigations even in that class give no account of what might be called a heterochromosome and it was not until after the discovery of sex chromosomes in other animals that claims of their occurrence in the molluscs began to appear.

In the order of the *Pulmonata* the first report of a heterochromosome was made in species of *Helix*. ZIEGLER ('08) and KLEINERT ('09) described a very large tetrad in the spermatocytes of that genus, but aside from the observation that it lagged on the spindle gave very little information that might justify the assumption that they had seen a sex chromosome. Soós ('10) reported in *Helix arbustorum* a pair of

m chromosomes and also an unpaired chromosome-like body which he believed was cast out into the cytoplasm in the course of the first spermatocyte division. He therefore regarded it not as a chromosome but as a true nucleolus. DEMOLL ('11, '12) however could find no trace of m chromosomes in *Helix pomatia* but became convinced that the body which Soós had regarded as a nucleolus is really a double chromosome and perhaps a tetrad composed of 2 X elements. This passes undivided to one pole in the first division and is not cast out as Soós had claimed. Only the sperms which arise from the cell carrying the heterochromosome or sex chromosomes are capable of fertilization. DEMOLL's evidence is clearly inadequate either for his more general conclusions or for a demonstration of the presence of sex chromosomes. It seems unfortunate that no more recent and adequate investigation is available in the *Pulmonata*, for the general occurrence of hermaphroditism in that group makes a knowledge of the sex chromosome conditions very desirable.

In another order, the *Opisthobranchia*, hermaphroditism is also the typical condition, and there the technical difficulties are apparently not as great as in the *Pulmonata*. As long ago as 1904 SMALLWOOD mentioned briefly an "accessory" chromosome which he had observed in the maturation of the eggs of *Haminea*, but gave no adequate description of it. In 1911 ZARNIK published a preliminary account of his studies in the group of pteropods, and in view of the fact that his remarkable conclusions have often been considered, a brief outline of his report may be given here. His main work was done on *Creseis* in which he found 18 large and 2 small chromosomes in the spermatogonial plates. In the first spermatocyte metaphase are found 9 large and 1 smaller tetrad, and whereas the former divide normally in both divisions, the smaller element goes undivided to one pole in the second division. Two types of sperms are thus formed, carrying 9 and 10 chromosomes respectively. In the maturation of the egg are found 8 large and 2 small elements, all dividing in both divisions. Since all cleavage figures were found to show 18 large and 2 small chromosomes, and all female pronuclei carry 8 large and 2 small chromosomes, ZARNIK concluded that only sperms carrying 10 large chromosomes are capable of fertilizing the eggs. According to ZARNIK this number of large chromosomes in the sperms is attained when in the second spermatocyte division the 2 small chromosomes do not divide, whereas the larger chromosomes all divide at that time. In this way all the chromosomes are brought to the same size. But this hypothesis, unsupported by actual evidence, does not cover all the peculiarities of the case, for the origin of the 8 large and 2 small tetrads in the egg from the diploid number of 18 large and 2 small chromosomes remains still to be accounted for. ZARNIK therefore assumed that in the female somatic cells there is somewhere a diminution of 2 large chromosomes which results in a chromosome set of 16 large and 4 small chromosomes (which could then form 8 large and 2 small tetrads). Finally ZARNIK assumed that the small chromosomes represent sex chromosomes and that two of these do not undergo diminution in the male as they do in the female. ZARNIK's promised detailed paper has never appeared (unless he so regards his 1913 account). As it stands, his account does not merit serious consideration, and SCHITZ ('16, '17, '25) indeed concluded

after a renewed investigation of certain pteropods that heterochromosomes are entirely lacking in those forms.

In the *Streptoneura* (*Prosobranchia*) cytological evidence on the occurrence of sex chromosomes is somewhat confused. In 1913 KUSCHAKEWITSCH figured a dividing chromosome showing a tendency to lag in the first spermatocyte spindles of *Conus mediterraneus*, and a similar

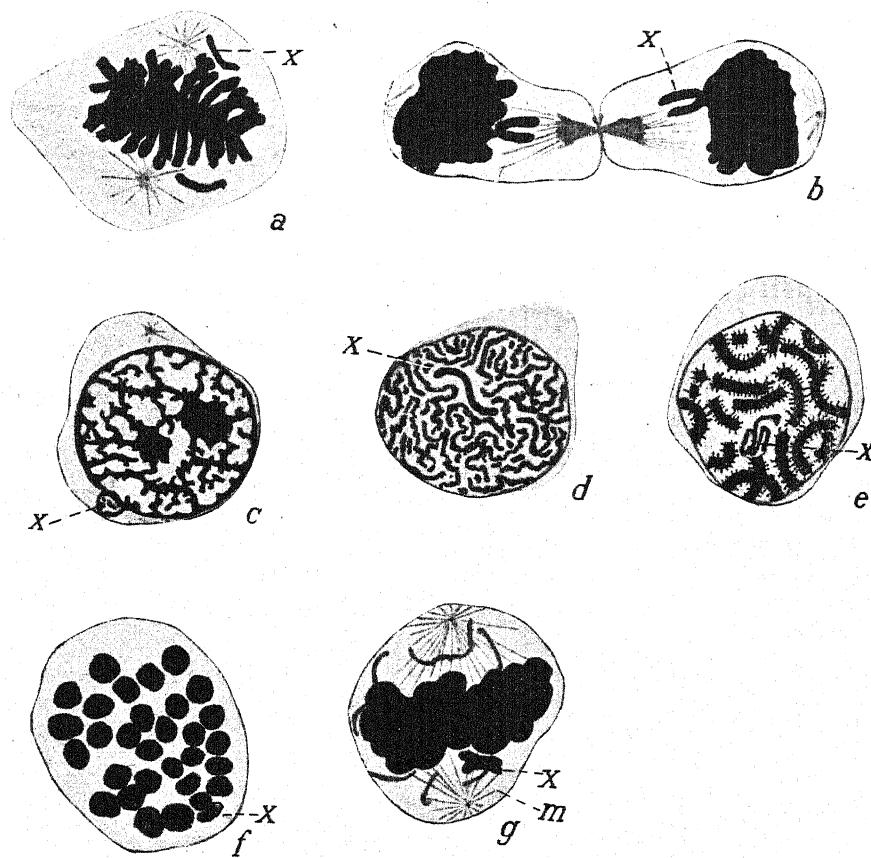


Fig. 14. *Fasciolaria tulipa* (HYMAN, '23)—*a* Spermatogonial metaphase. *b* Spermatogonial anaphase. *c* Resting phase of first spermatocyte. *d* Leptotene stage of first spermatocyte. *e* Pachytene stage of first spermatocyte. *f* Polar view of first spermatocyte metaphase. *g* Side view of first spermatocyte division.

chromosome in the second spermatocyte divisions of *Vermetus gigas*. He ascribed no special significance to this behavior at the time, but in a paper ('24) written shortly before his death he described heterochromosomes or as he termed them, "allosomes", in 8 different species. Since he tended to believe that these allosomes divided equationally in both spermatocyte divisions, he was forced to purely hypothetical assumptions in order to explain how the chromosome number is kept constant.

## MOLLUSCA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Ceritium vulgatum</i>	—	—	—	—	One heterochromosome	KUSCHAKE-WITSCH '24
<i>Columbella rustica</i>	—	16 +	—	—	One heterochromosome	SCHITZ '16 KUSCHAKE-WITSCH '24
<i>Conus europaeus</i>	—	—	—	—	One heterochromosome	KUSCHAKE-WITSCH '24
<i>Conus mediterraneus</i>	—	14	14	—	One lagging chromosome in first division	KUSCHAKE-WITSCH '13
<i>Crescis acicula</i>	20 oog. 20 spg. 20 embryo.	10 10 ♀	10 10 ♀	9 10 10 ♀	Status of sex chromosomes not clear	ZARNIK '11, '13
<i>Fasciolaria tulipa</i>	—	30? + X	—	—	X to pole in 1st	HYMAN '28
<i>Haminea solitaria</i>	—	16 ♀	16 ♀	—	One heterochromosome?	SMALLWOOD '04
<i>Helix arbustorum</i>	48? spg.	24	24	—	One heterochromosome?	Soós '10
<i>Helix pomatia</i>	48 spg.	24	23 24	—	One tetrad to pole in 1st = X <sup>I</sup> X <sup>II</sup> ?	DEMOLL '11, '12
<i>Hyalea tridentata</i>	24	—	—	—	Heterochromosome to pole in 1st (X?)	ZARNIK '11
<i>Hyalocylis striata</i>	24	10 + X <sup>I</sup> + X <sup>II</sup>	10 + X <sup>I</sup> + X <sup>II</sup>	10 10 + X <sup>I</sup> + X <sup>II</sup>	Identification of sex chromosomes uncertain	ZARNIK '11, '13
<i>Marsenia</i> sp.	—	—	—	—	2 heterochromosomes in male?	KUSCHAKE-WITSCH '24
<i>Nassa mutabilis</i>	—	—	—	—	2 heterochromosomes in male?	KUSCHAKE-WITSCH '24
<i>Neretina fluviatilis</i>	—	—	—	—	1 heterochromosome in male?	KUSCHAKE-WITSCH '24
<i>Tiedemannia neapolitana</i>	28 spg.	—	—	—	Heterochromosome (X?) to pole in 2nd	ZARNIK '11
<i>Turitella communis</i>	—	—	—	—	2 unequal heterochromosomes (XY?) to opposite poles in 1st	BATAILLON '24
<i>Turitella tereba</i>	—	—	—	—	2 heterochromosomes?	KUSCHAKE-WITSCH '24
<i>Turitella triplicata</i>	—	9—11	—	—	1 heterochromosome?	SCHITZ '20
<i>Vermetus gigas</i>	—	14	14	—	1 lagging chromosome in 2nd	KUSCHAKE-WITSCH '13, '24

SCHITZ ('16, '20) stated that he had been unable to establish the presence of heterochromosomes in *Columbella rustica* (one of the forms in which KUSCHAKEWITSCH reported allosomes) but described in the first spermatocyte of *Turitella triplicata* a chromosome which precedes the others in going to one pole. Whether this chromosome is unpaired or whether it is the precocious member of an otherwise normal pair of chromosomes is difficult to tell from his figures. In the allied species, *Turitella communis*, BATAILLON ('21) described an unequal pair which, separating in the first spermatocyte division, precedes the other chromosomes to the poles. This behavior suggested an XY pair to BATAILLON. But the best evidence on sex chromosomes was given by HYMAN ('23) who was able to trace a heterochromosome through the spermatogonial and first spermatocyte stages of *Fasciolaria tulipa* (fig. 14). In the former, it divides and begins its journey to the poles while the remaining chromosomes are still in the plate. But peculiarly enough, it pauses before reaching the pole, so that the other chromosomes divide and reach the poles while the heterochromosome is still lagging. Its behavior in the preparatory phases of the spermatogonia and spermatocytes is quite characteristic, for it then lies definitely outside the nucleus although in contact with its periphery. (KUSCHAKEWITSCH described a similar position for his allosome, although in some cases he showed it far removed from the nucleus.) HYMAN showed that the chromosome in question forms a long dense rod at the time when the other chromosomes have assumed the shape of long leptotene threads. After the synapsis stage, in which it can of course not take part, it appears as a string of chromomeres, but finally condenses and lies at one side of the fully formed chromosome plate. Going undivided to one pole in the first division, its exact behavior in the second could not be followed, although HYMAN assumes that it then divides equationally. In this case at least therefore there is a strong indication that the heterochromosome concerned is a sex chromosome and that the XO condition characterizes the male. But it must be pointed out that even here the difficulty of making dependable chromosome counts and the technical obstacles which make a detailed study of the forms and size of chromosomes almost impossible militate against reaching a final conclusion.

## ARTHROPODA

### CRUSTACEA

In no member of this class has a conclusive demonstration of sex chromosomes been furnished as yet. Indeed, it is not certain which sex is heterogametic — although recent studies indicate that as in most other animals it is the male. As might be inferred from this, conditions are by no means favorable to cytological investigation, and this is especially true in the Entomostraca where so many interesting but puzzling observations in regard to the life cycle have been made and might be cleared up if only the cytology were better known.

No heterochromosomes of any kind have been observed in the *Ostracoda* (SCHLEIP, '09; MÜLLER-CALE, '13), the *Cirripedia* (KRÜGER, '20), and the *Phyllopoda* (KÜHN, '08). In the last named order,

two accounts of the spermatogenesis are available — on *Simocephalus* (CHAMBERS, '13) and *Daphnia* (TAYLOR, '14). But neither author throws any light on the question of sex chromosomes, nor is the possibility that the males are haploid convincingly disposed of. It is only in the remaining order of the Entomostraca, the *Copepoda*, that there is evidence of heterochromosomes, but their exact nature in this group is still in doubt. In the egg of *Cyclops fuscus* var. *distinctus*, both BRAUN ('09) and MATSCHEK ('10) have described beside 5 ditetrads a

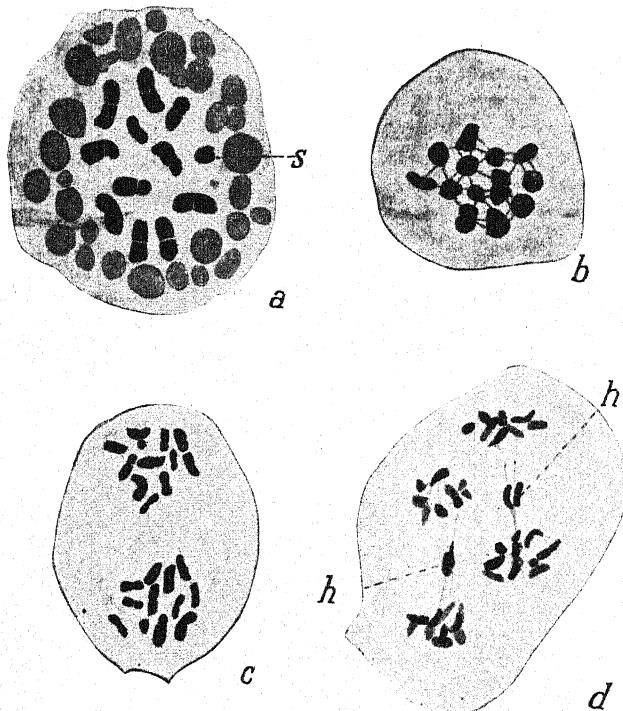


Fig. 15. *Hersilia apodiformis* (KORNHAUSER, '15)—*a* Metaphase of first oocyte division with one tetrad (*s*) showing no Querkerbe. *b* Metaphase of first spermatocyte showing 11 autosomal tetrads and 2 unpaired heterochromosomes. *c* Two second spermatocyte metaphases. *d* Two second spermatocyte anaphases showing lagging heterochromosomes (each already split).

single, smaller tetrad which does not show the Querkerbe which characterizes the others and gives rise to their name. This tetrad goes undivided to one pole in the first maturation division. AMMA ('11) believed that in some embryos of this species the diploid number of chromosomes is 11, the odd number suggesting the presence of a sex chromosome which might correspond to the heterochromosome described by BRAUN and MATSCHEK. Similar heterochromosomes were found by these workers in maturing eggs of *Cyclops affinis*, *C. prasinus*, *C. phaleratus*, and in some cases of *C. vernalis*. It is clear that if these observations are correct, it is possible that we are indeed dealing with a sex chromo-

some, and its behavior would furthermore suggest that in these species it is the female that is heterogametic.

A similar hypothesis does not seem possible in the case of *Hersilia apodiformis* (KORNHAUSER, '15). Both spermatogonia and oogonia here show 22 tetradlike chromosomes (they appear as tetrads because of the presence of a Querkerbe, but this is of no significance in the meiotic divisions, if KORNHAUSER is correct) plus 2 chromosomes of the simple type (i. e. without Querkerbe). In the egg pseudoreduction leads to 12 true tetrads, 11 of which still show the Querkerbe. The course of the maturation divisions in the egg was not described. In the spermatocytes there are usually 11 tetrads and 2 unit chromosomes. The latter occasionally pair (in about a fourth of the cases), but whatever their

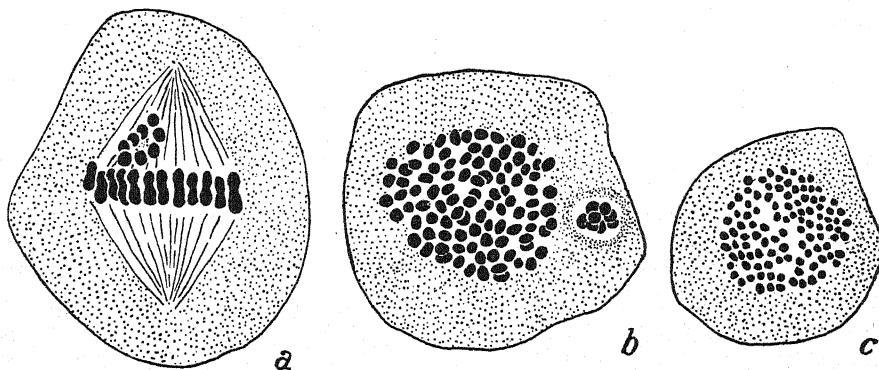


Fig. 16. *Cambaris immunis?* (FASTEN, '14)—*a* Metaphase of first spermatocyte showing clump of eight heterochromosomes preceding autosomes to the pole. *b* Polar view of first spermatocyte metaphase showing 96 autosomes and a clump of 8 heterochromosomes. *c* Polar view of second spermatocyte metaphase, showing 104 chromosomes and no visible distinction between autosomes and heterochromosomes.

behavior in this respect, they always pass to opposite poles in the first spermatocyte division. Since the second division seems to be equational, all spermatids therefore receive 11 ordinary chromosomes and 1 heterochromosome (fig. 15). It will be apparent that the behavior of the pair of heterochromosomes suggests an XY pair, so that in this case the male would be heterogametic. But it must not be forgotten that until the account of the maturation in the egg and the consequent fertilization and cleavage is complete, no final decision on this point is justified.

HEBERER ('24) found that in *Anomalocera*, *Diaptomus salinus*, and *Heteropece weismanni* certain irregularities appear in some of the chromosomes in the spermatogenesis. Especially noteworthy is the tendency on the part of one tetrad (a dyad in case of *Anomalocera*) to remain separated from the metaphase plate of the first spermatocyte. Some of his figures suggest that the tetrad is already on its way to the pole and that therefore we are dealing with a precession of this element, but HEBERER's data do not throw any further light on the nature of this heterochromosome.

## CRUSTACEA

Species	Diploid Chromo-some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Cambarus immunis</i>	—	104	96 104	—	X of 8 components in the male	FASTEN '14
<i>Cyclops affinis</i>	—	7 ♀	—	—	1 heterochromosome in female	MATSCHEK '10
<i>Cyclops fuscus</i> (var. <i>distinctus</i> )	11 in some embryos	6 ♀	—	—	1 heterochromosome in female	BRAUN '09 MATSCHEK '10 AMMA '11
<i>Cyclops phaleratus</i>	18 clv.	7 ♀	6 ♀ 7 ♀	6 ♀ 7 ♀	1 heterochromosome in female	MATSCHEK '09, '10 BRAUN '09
<i>Cyclops prasinus</i>	—	6 ♀	—	—	—	BRAUN '09 MATSCHEK '10
<i>Cyclops serrulatus</i>	14 oog.	8 ♀?	—	—	2 heterochromosomes in female?	BRAUN '09 MATSCHEK '10
<i>Cyclops vernalis</i>	10 oog.	5 ♀ 6 ♀	—	—	A heterochromosome may or may not be present	BRAUN '09 MATSCHEK '10
<i>Diaptomus castor</i>	34 clv.	15 ♀	17 ♀	17 17 ♀	3 chromosomes fuse in 1st oocyte	HÄCKER '08 MATSCHEK '09, '10 AMMA '11
<i>Gammarus chevreuxi</i>	26 spg. 26 approx. ♂ soma	—	—	—	XY in male?	PALMER '25, '26
<i>Hersilia apodiformis</i>	24 oog. 24 spg. 24 clv.	12 or 13 12 ♀	12	—	2 heterochromosomes in male may or may not pair in 1st. They go to opposite poles in 1st	KORNHAUSER '15

To a slightly different category belongs BRAUN's account of meiosis in the egg of *Cyclops serrulatus* ('09). The preparatory phases show among the ordinary chromosomes, 2 smaller chromosomes. These go to opposite poles in the first division, and this division is therefore reductional as far as they are concerned. But BRAUN claimed that that member of the pair that did not pass out into the first polar body may either pass out into the second polar body or remain in the egg undivided. This would present the peculiar condition of a chromosome subjected to

two reduction divisions for which the existing evidence is entirely inadequate. Finally may be mentioned the case of *Diaptomus castor* (MATSCHÉK, '10) where in the meiosis of the egg 3 tetrads together form a ring. Here, as in nearly all the preceding cases, the data are not complete and nothing is known of the significance of the phenomenon.

Passing to the group of Malacostraca mention should be made of FASTEN's ('14) observations on *Cambarus immunis* (fig. 16) where the first spermatocyte metaphases show 104 elements of which 8, lying in a distinct vacuole, are usually separated from the rest. In the first spermatocyte division this entire group goes to one pole while the other chromosomes divide normally. As a result half of the second spermatocytes contain 96 and the other half 104 chromosomes. At this time the grouping of the 8 special elements or heterochromosomes is lost and thereafter it is impossible to distinguish them from the other chromosomes. Unfortunately FASTEN did not make a complete study of the spermatogenesis nor did he investigate the oogenesis, his chief attention being directed to another species of *Cambarus*.

The occurrence of an XY pair of sex chromosomes has recently been reported for the male *Gammarus chevreuxi* by PALMER ('25). The very brief preliminary paper does not however give his evidence for this claim<sup>1</sup>.

It will be apparent that the whole question of sex chromosomes in the Crustacea is still unsettled. Heterochromosomes certainly occur, at least in the Copepoda and two of the Malacostraca. But since in the former they have been described in both sexes, and as in no case a complete cytological analysis has been made it is at present impossible to identify them as sex chromosomes.

#### MYRIAPODA

No species in this class of *Arthropoda* has been subjected to an adequate analysis in regard to sex chromosomes, although some interesting observations are available. BLACKMAN's studies on *Scolopendra heros* (fig. 17A + B) and *S. spinipes* are perhaps the most thorough. In both species the males seem to be of a simple XO type and two kinds of spermatids (16 and 16 + X) are formed. The odd chromosome, almost certainly the X, is recognizable already in the preparatory phases of the spermatogonia where it remains condensed and does not become diffuse like the autosomes. Similar behavior characterizes it in corresponding stages of the spermatocytes, where it also serves as a center in the characteristic karyosphere formation so often observed in these forms. According to most observers the karyosphere is formed by the aggregation of all the autosomal threads around the sex chromosome, the whole finally forming a more or less irregularly staining, round lump. The chromosomes reappear from the karyosphere as bivalent threads—except for the X, which as already noted, has no partner and remains compact. BLACKMAN's less detailed account of the spermatogenesis in

<sup>1</sup> PALMER's more detailed paper ('26) strengthens his claim but it contains no information on the behavior of the heterochromosomes in the prophases nor does it give any evidence on the chromosomes of the female.

three species of *Lithobius* indicates that there conditions similar to the preceding obtain, but that technically these animals are not so favorable for an analysis of the chromosomes. In none of his papers did BLACKMAN give any data in regard to the chromosomes of the female or the somatic cells of the male, and MEDES ('05) makes a similar omission in her report on *Scutigera forceps*. There is however little doubt that the males of the last named form also represent the XO condition. BOUIN and ANCEL ('11) working on another species of the same genus (*S. coleoptrata*) also reported the XO condition for the males, but believed that the sex chromosome divides in both spermatocyte divisions. In a series of more recent papers, BOUIN ('20, '22, '25) reaffirmed and added to this earlier work. He was unable to count exactly the chromosomes of *Scolopendra cingulata*, but finally concluded that the spermatogonial number must lie between 28 und 32, without counting the heterochromosomes. In the preparatory phases of the spermatocytes he was able to demonstrate the synaptic stage which had escaped BLACKMAN, but agreed in general with the earlier workers on the subject of karyosphere formation. Although he was unable to follow the heterochromosome in the spermatocyte divisions, he concluded (apparently merely because it does not stand out at this time) that it divides in both divisions. As a result each of the four spermatids resulting from the two divisions of a first spermatocyte carries the chromosome in question, so that on the basis of these observations it could hardly function as a typical sex chromosome. BOUIN's hypothesis of sex determination in this animal therefore is based on an entirely different view point. As BLACKMAN had already mentioned earlier, there appear to be two lines of germ cells which although alike in the general structure of their chromosomes, differ distinctly in size. BOUIN's suggestion is that the larger line of cells gives rise to female producing sperms, the smaller to male producing sperms. This hypothesis, with little evidence to support it, necessitates subsidiary hypotheses, such as a separation of the large from the small elements in the males, and a subsequent redoubling of the chromosomes thus separated. It seems unnecessary to comment on these purely speculative aspects of BOUIN's work, but a reexamination of the so called heterochromosome is urgently called for even though it seems unlikely, in case BOUIN's observations are correct, that it is identical with the X chromosome described in other forms by BLACKMAN and MEDES.

All the preceding species belong to the order of *Chilopoda*. The only other account in which sex chromosomes have been described is that of OETTINGER ('09, '10) on the diplopod *Pachyiulus varius*. Again only the spermatogenesis was described, a fact especially to be regretted because some very interesting special features appear in this instance. In general, no difference from the spermatogenesis of *Chilopoda* seems to obtain here. The karyosphere is formed in a similar manner, and an unpaired heterochromosome, very probably an odd X, goes to one pole in the first spermatocyte division. The exceptional features do not especially concern the sex chromosome. Their peculiarity lies chiefly in such observations as the following: the chromosomes reappear from the karyosphere in the diploid, not the haploid number; they nevertheless look like tetrads; in the metaphase plate of

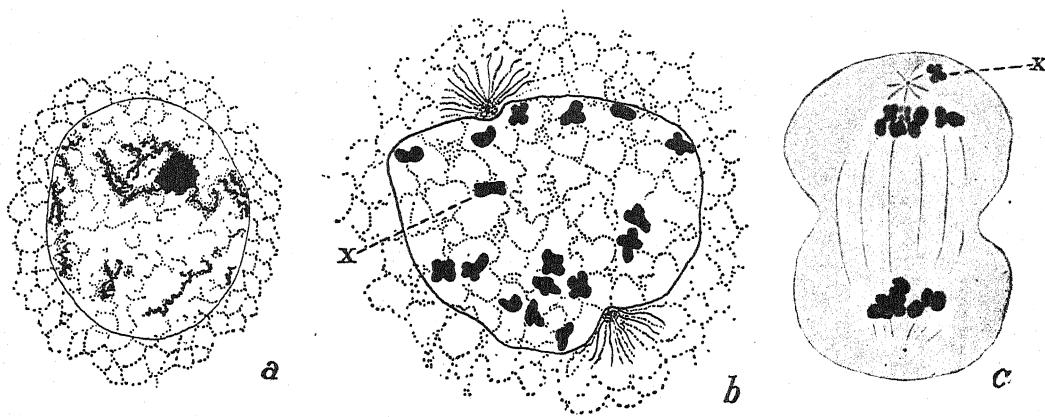


Fig. 17. *Scolopendra heros* (BLACKMAN, '03)—*a* First spermatocyte showing origin of chromosomes from karyosphere. *b* First spermatocyte with split X and the autosomes evolved. *Pachyulus varius* (OETTINGER, '09)—*c* Figure showing tetrad structure of X in first spermatocyte division.

### MYRIAPODA

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Lithobius mordax</i>	—	24 + X	—	—	—	BLACKMAN '07
<i>Lithobius mutidentatus</i>	—	24 + X	—	—	—	BLACKMAN '07
<i>Lithobius</i> sp.	—	24 + X	—	—	—	BLACKMAN '07
<i>Pachyulus varius</i>	25 spg.	13	13 12	13 12	X is tetrad in form	OETTINGER '08, '09
<i>Scolopendra cingulata</i>	28—30 spg.	14—16	14—16	14—16	—	BOUIN '20, '22, '25
<i>Scolopendra heros</i>	33 spg.	16 + X	16 16 + X	16 16 + X	—	BLACKMAN '03, '05a, '10
<i>Scolopendra subspinipes</i>	—	—	—	—	In male X to pole in 1st	BLACKMAN '05a
<i>Scutigera coleoptrata</i>	—	17 + X	—	—	Believe X divides in both divisions	BOUIN & ANCEL '11
<i>Scutigera forceps</i>	37 spg.	18 + X	18 18 + X	—	—	MEDES '05

the first division they appear as octads, and they are then in the haploid number. Whether we are here dealing with a Querkerbe such as has given rise to so much confusion in various Crustacea and Nematoda, or whether we are concerned with a special development, can not be ascertained (fig. 17 C). SOKOLOFF ('14) working on *Polyxenus* does not seem to have observed anything similar to it, and SILVESTRIS ('02) in his work on fertilization in the eggs of Myriapoda likewise makes no mention of it.

All in all, it is probable that in Myriapoda the males are heterogametic and that they are usually of a simple XO type. Study of the diploid sets of chromosomes in both sexes as well as of oogenesis are however necessary before this can be regarded as definitely established.

#### INSECTA

In no other class of animals has so much information about the sex chromosomes been gathered as in this one. There is an astonishing number and range of observations, and it is no exaggeration to say that most of our knowledge about sex chromosomes is based on work done on the insects. For the sake of easier comprehension it has been necessary to treat the orders and in some instances the families separately.

#### APTERA

To my knowledge, the only species of this order in which sex chromosomes have been reported is *Lepisma domestica*. CHARLTON ('21) reported 34 chromosomes in the spermatogonial cells, 2 of these chromosomes tending to remain condensed during the resting and preparatory stages. During the growth and prophases the last named chromosomes often break up into irregular masses which in turn give rise to threads easily distinguishable from the autosomal threads because of their more intensive staining. It is during or following this stage that there is an end to end union of the two threads in question and very often the larger comes in contact with a plasmosome then present.

The metaphase plate of the first spermatocyte finds 18 chromosomes. The 2 heterochromosomes just described are usually connected with each other through a short thread, and pass together to one pole without becoming separated. Although CHARLTON's figures of the second spermatocyte division are not decisive in this respect, it appears to me probable that the heterochromosomes divide equationally at that time. However, this point is not clear.

CHARLTON's conclusions were somewhat confusing. He evidently believed that he was dealing with a compound X of two elements and therefore classified *Lepisma* with *Syromastes* in which WILSON had demonstrated the  $X^I X^{II} O$  condition for the male. Nevertheless he definitely stated in his description that after going together to one pole in the first division, the 2 heterochromosomes separate and pass to opposite poles in the second division. It is plain that if this description is followed literally, three types of sperms would be formed ( $16, 16 + X^I$ , &  $16 + X^{II}$ ). An examination of female material and reexamination of the male is evidently in order.

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Lepisma domestica</i>	34 spg.	16 + X <sup>I</sup> + X <sup>II</sup>	16 + X <sup>I</sup> + X <sup>II</sup> 16	16 + X <sup>I</sup> + X <sup>II</sup> 16	CHARLTON's account is self-contradictory as to divisions	CHARLTON '21

## ORTHOPTERA

So much work touching on sex chromosomes has been reported in this order and so much diversity is found to occur in the cytological behavior of the different families that a treatment of the whole order as a single unit would certainly prove too cumbersome.

*Acrididae*: The number of chromosome studies in this one family is a very large one. CAROTHERS, DAVIS, MC CLUNG, ROBERTSON, WENRICH and many others have made very painstaking analyses of the chromosome conditions in various species, and on the knowledge so gained rest a great many of our present conceptions about that aspect of animal cytology. The uniformity of the chromosomal phenomena as met in this particular family is surprisingly great. By far the largest number of species shows the diploid numbers of 23 and 24 for the male and female respectively. Nearly all the exceptions are to be encountered in the subfamily Tettiginae, and here again the numbers encountered (13 and 14 for male and female) are in themselves remarkably constant for different species of that group. A similar uniformity is to be found in the behavior of the sex chromosomes. In every case the male shows the XO and the female the XX condition. Usually the sex chromosome is one of the larger chromosomes (often the third or fourth largest). It is conspicuous in the growth stages of the spermatocyte and often also in the spermatogonial cell because of heteropycnosis, while in the metaphase plate it is often easily recognizable through a slightly roughened outline. In almost every detailed analysis it has been remarked that during certain stages the chromosomes are contained in vesicles which so far as the autosomes are concerned may often fuse with each other at the extremities while that of the sex chromosome is set slightly apart and maintains its individuality. The vesicles are prominent especially during the spermatogonial stages, in most cases disappearing only during the actual division (fig. 18). In a few cases (WENRICH, '17) so-called "chromomere vesicles" have been observed in connection with the sex chromosomes during the growth and prophanes. They have been interpreted as reservoirs for chromatin, loosing and regaining their stainability at different periods but always in contact with a certain chromosome (fig. 18K). However, whatever their significance, they are not specifically associated with the sex chromosomes only, but have been seen in connection with autosomes as well (CAROTHERS, '13).

The X always passes undivided to one pole in the first and divides equationally in the second spermatocyte division. The study of the

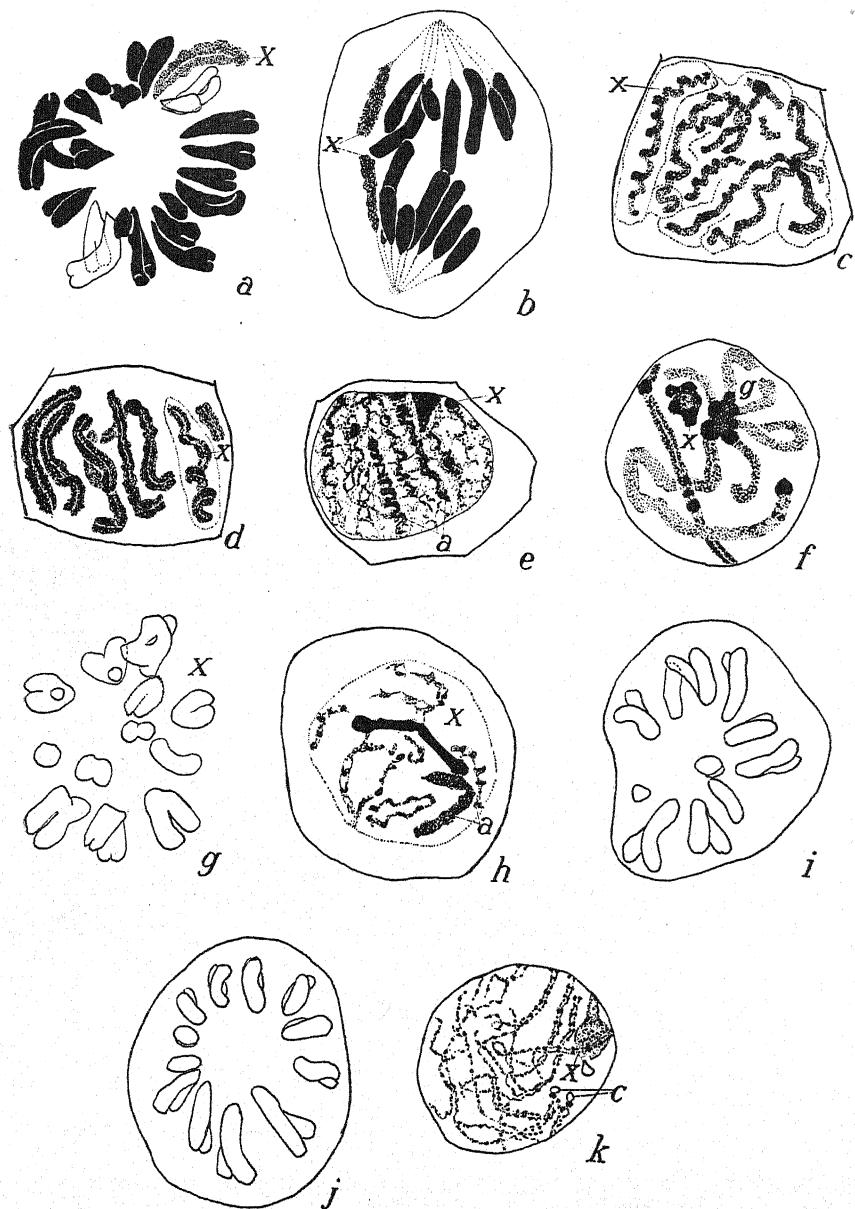


Fig. 18. *Phrynotettix magnus* (WENRICH, '16)—*a* Spermatogonial metaphase. *b* Spermatogonial anaphase. *c* Spermatogonial prophase. *d* Late spermatogonial prophase. *e* Pre-leptotene stage of first spermatocyte (*a* = pair of autosomes). *f* Pachytene stage of first spermatocyte (*g* = composite granule breaking up into polar granules). *g* Metaphase of first spermatocyte. *h* Interkinetic stage. *i* Metaphase of second spermatocyte with 11 chromosomes. *j* Metaphase of second spermatocyte with 12 chromosomes. *Chorthippus curtipennis* (WENRICH, '17)—*k* Zygote stage of first spermatocyte showing chromomere vesicles on X and autosomes (*c*).

maturation in the eggs unfortunately meets with technical difficulties so that up to the present time no adequate account of it is available. However the chromosomes in the female have been open to study in somatic and younger germ cells so that no doubt of the actuality of an XX pair of sex chromosomes in that sex is possible.

Departures from the common types of diploid complexes can in most instances be traced to a fusion of certain chromosomes, sometimes as early as the spermatogonia. Usually such a fusion takes place end to end. The smaller number of chromosomes observed in such cases is therefore only an apparent reduction. It is of interest to note that such fusion may sometimes occur between the sex chromosome and a certain autosome. No effect on the behavior of chromosomes thus associated can be noticed, the X condensing precociously in the spermatogenesis while the associated autosome behaves like the unattached autosomes. In some cases like *Chorthippus curtipennis* (ROBERTSON, '16)

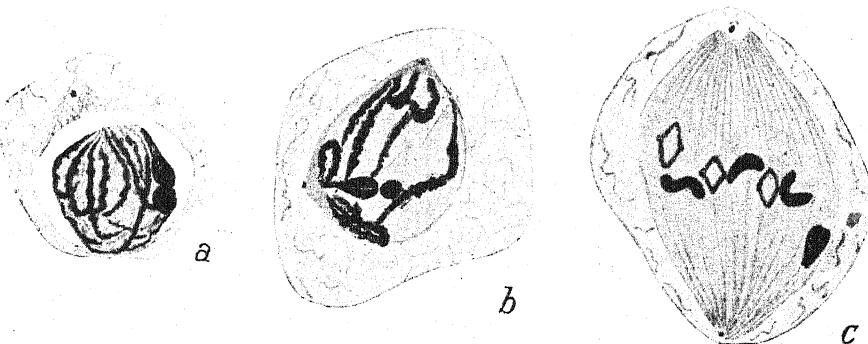


Fig. 19. *Periplaneta americana* (MORSE, '09)—*a* Synaptatene stage of first spermatocyte. *b* Early diakinesis in first spermatocyte. X showing split and attached spherical plasmosome. *c* Anaphase of first spermatocyte, with X preceding autosomes to pole.

the X although always in contact with an autosome during the preparatory phases of the spermatocytes, finally becomes separated in the metaphase of the first spermatocyte division. In other cases like *Hesperiottix* (MC CLUNG, '05, '07) the association seems more or less permanent (fig. 9).

Numbers larger than those commonly encountered are usually brought about by the presence of supernumeraries. Their exact origin is not known although it seems likely that they arise through some process akin to non-disjunction.

*Blattidae*: MOORE and ROBINSON ('04) thought that in the male of *Periplaneta* the chromatin nucleolus as seen in the spermatogonial and spermatocyte prophases is not identical with a sex chromosome, and then went so far as to doubt the existence of sex chromosomes in general. However already in 1905 Miss STEVENS showed that in the closely related *Blatta germanica* there is an unpaired odd chromosome which is distributed to only half the second spermatocyte cells. WASSILIEFF ('07) could confirm the numerical results obtained by STEVENS, although he harshly criticized her work on several subsidiary

points — notably in regard to the plasmosome associated with the chromosome nucleolus during the growth stages of the spermatocytes. However, MORSE's careful comparative study ('09) of several Blattidae (fig. 19) showed that WASSILIEFF's own description of the behavior of the chromatin nucleolus had been erroneous, that the plasmosome and chromatin nucleolus are connected with each other until the metaphase of the first spermatocyte, that the plasmosome then comes to lie outside of the spindle and that the chromatin nucleolus, contrary to MOORE and ROBINSON, does indeed give rise to the sex chromosome. In all four of the forms investigated by MORSE, the X passes to one pole in the first spermatocyte division. Finally, as WASSILIEFF had already shown, the diploid number of chromosomes in the female is always greater by one chromosome than the diploid number of the male. The female therefore has the formula XX and the male XO.

*Gryllidae*: Except for one genus, the forms here included represent orthodox sex chromosome conditions, in which the males carry an unpaired X and the females 2 X. In the spermatogenesis the X goes undivided to one pole in the first and probably divides equationally in the second spermatocyte division. It seems worthy of mention that it was in the oogenesis of one of these forms, *Gryllus campestris*, that BUCHNER ('09) reported a body which he interpreted as an unpaired sex chromosome. Since he believed that a body identical with this is present also in the spermatogenesis, he concluded that the so called sex chromosome can have no function in the determination of sex. A prolonged controversy arose on these findings and it now seems certain that the body seen by BUCHNER in the cells of the female is not identical with a true sex chromosome as seen in the males, a fact brought out especially by GUTHHERZ ('07, '08, '09) and according to MOHR ('15) now conceded by BUCHNER himself.

More unusual conditions obtain in both of the species of *Gryllotalpa* that have been investigated. In *G. borealis* (fig. 20), PAYNE ('12b, '16) reported a spermatogonial number of 23 and an oogonial of 24 chromosomes (BAUMGARTNER, '12, may have also had this species). 12 bodies are found in the first spermatocyte plate, including an unequal bivalent or tetrad and one large, unpaired chromosome. In the first spermatocyte division the larger member of the unequal bivalent always passes to the same pole as the unpaired chromosome, whereas the smaller member of the bivalent goes to the opposite pole. The second division is equational for all chromosome. PAYNE tentatively interprets the unequal pair as an XY and the unpaired large chromosome as an odd X. Although on the available evidence no final conclusion is warranted, it seems possible that the unequal pair does not represent sex chromosomes at all but an unequal or heteromorphic pair of autosomes. This leaves open the question of why the large member of this pair should always pass to the same pole as the odd large element. It may be pointed out that the case does not stand isolated in this feature, for a similar occurrence has been noted by WALTON ('24) in the nematode *Physaloptera*.

Still greater complications are encountered in the case of *G. vulgaris*. PAYNE ('16) has shown that a great deal of confusion in that case arises from the fact that different European races of the species

have different chromosomal conditions. VOINOV ('12, '14a, '14b, '16) working with specimen from the vicinity of Bucharest first stated that the spermatogonial number is 14, but later qualified this report following the discovery that some cells showed 15 chromosomes. In the metaphase of the first spermatocyte he reported 7 bodies, 3 of which deserve special mention (fig. 20D). They are an L shaped chromosome (which VOINOV believes to be an autosomal tetrad connected with an "accessory" i. e. a hexad); an unequal pair (called an XY by VOINOV); and a small, dumbbell shaped bivalent (VOINOV's microchromosomes). To make a logical connection between the spermatogonial counts and the chromosomes as reported in the first spermatocyte, VOINOV was forced to conclude that the 2 microchromosomes form a bivalent already in the

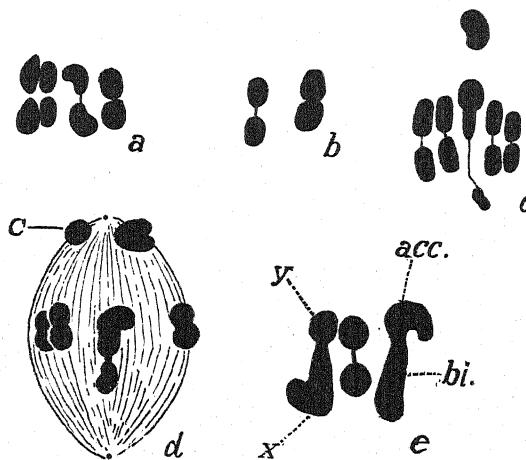


Fig. 20. *Gryllotalpa borealis* (PAYNE, '16)—a, b & c First spermatocyte division, showing all the chromosomes of a single figure. d First spermatocyte division showing X and chromatoid body (c) at one pole. *Gryllotalpa vulgaris*—e The three questionable chromosomes in the first spermatocyte division, with VOINOV's interpretation.

spermatogonia and appear there as a single chromosome; that the smaller member of his XY pair escapes detection during the same period; and finally that one of the spermatocyte chromosome bodies is really an octad (composed of 4 split autosomes) and not a true tetrad. This would give a total of 17 spermatogonial chromosomes of unit value. SENNA ('11) had indeed reported this number previously, but instead of 7 had found 9 chromosomal bodies in the first spermatocyte. VOINOV's many assumptions have too little support in actual observations to merit any extended consideration at this time. PAYNE pointed out this lack of evidence for VOINOV's conclusions and showed further that VOINOV could hardly have interpreted his hexad element correctly if the accessory and its associated autosomal tetrad go to opposite poles in the first division. This would bring about the unprecedented case of an autosomal tetrad dividing in only one of the meiotic divisions. PAYNE and also CAROTHERS ('16) prefer to interpret VOINOV's hexad or L shaped chromosome as a tetrad of asymmetric shape, being formed per-

haps by a pair of heteromorphic autosomes. His XY pair on the other hand may represent such a hexad, its composing elements being an autosomal tetrad joined with an X. This would give *Gryllotalpa* males an odd or unpaired X chromosome. However it seems evident that VOINOV's m chromosomes as well as his other peculiar elements should be reexamined, not only in the Bucharest race but also in other strains, and also that the chromosomes of the female should be studied carefully instead of being entirely neglected<sup>1</sup>.

*Locustidae* (Tettigoniidae): Although generally speaking, the cytological conditions in this family are not as favorable as in some other Orthoptera, the great size which makes the sex chromosome so conspicuous in many of the species of the locustids made them some of the first objects to be taken up in connection with this element. Already in 1899 McCLEUNG had noticed the large X in the males of *Xiphidium* and called it the "accessory" chromosome, and within two years DE SINETY gave a further account of the behavior of this chromosome in a few other species of the family. In spite of this early work almost no exhaustive account of the chromosome cycle in one of the Locustidae has been reported, MOHR's studies of *Locusta viridissima* and *Leptophyes punctatissima* being the only ones which take up a more detailed analysis of the chromosomes in the female as well as the exact behavior of the X in the male somatic and germ cells (fig. 3 and 4). However, the chromosomal phenomena appear to be so uniform throughout the family that it seems safe to assume that even in the less thoroughly investigated forms the behavior of the chromosomes does not depart in any important respect from that observed in a case like *Locusta*.

In every case investigated, the sex chromosome formula for the female is XX and for the male XO. In the latter, the X passes to one pole in the first and divides equationally in the second division. At nearly all stages except that of actual division, the X is contained in a special vesicle apart from those of the autosomes. MOHR ('15, '16) was convinced that its behavior in general parallels that of the autosomes during the preparatory phases and that its precocious condensation during that time is due entirely to the fact that it has no partner with which it can go through the evolutions witnessed in the autosomes (fig. 4).

In this family also occurs the peculiar association reported in various other animals, between the X and an autosome. In *Anabrus*, McCLEUNG ('05) reported the sex chromosome of the male as united with one of the autosomes, not only in the germ but also the somatic cells.

*Mantidae*: OGUMA's work on the closely related forms *Paratenodera* and *Tenodera* ('21) shows that in the males of both species there are 3 sex chromosomes — 2 unequal X elements and a relatively small Y. In the preparatory phases of the first spermatocyte these 3 sex chromosomes form a single, compact chromosome nucleolus from which they reevolve as the first metaphase is approached (fig. 21). During this process the two components of the X first tend to form threads whereas

<sup>1</sup> Very recently (1925) VOINOV has stated that the spermatogonial number may vary from 14 to 16, but that does not explain all the peculiarities of the case.

## ORTHOPTERA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<b>1. ACRIDIDAE</b>						
<i>Acridium granulatus</i>	13 spg. 14 oog.	6 + X	6 6 + X	—	—	ROBERTSON '15, '16
<i>Acridium incurvatus</i>	13 spg.	—	—	—	—	ROBERTSON '16
<i>Acridium obscurus</i>	13 spg.	6 + X	—	—	—	ROBERTSON '16
<i>Acridium ornatus</i>	—	6 + X	—	—	—	ROBERTSON '16
<i>Acrolophitus</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MC CLUNG '14
<i>Aeoloplus</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MC CLUNG '14
<i>Amphitornus</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MC CLUNG '14
<i>Arphia pseudonietana</i>	23 spg.	—	—	—	Male = XO	MEEK '13b
<i>Arphia simplex</i>	23 spg.	11 + X	—	—	—	CAROTHERS '13
<i>Arphia tenebrosa</i>	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	DAVIS '08
<i>Arphia</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MC CLUNG '14
<i>Aulocara</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MC CLUNG '14
<i>Boopedon</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MC CLUNG '14
<i>Brachystola magna</i>	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	SUTTON '00, '02 CAROTHERS '13
<i>Camnula pellucida</i>	23 spg.	11 + X	11 11 + X	—	1 or 2 super- numeraries often present	CARROLL '20
<i>Camnula</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MC CLUNG '14
<i>Chloealtis</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MC CLUNG '14
<i>Chorthippus (Ste- nobothrus) bicolor</i>	17 spg.	8 + X	8 8 + X	—	—	MEEK '13b

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Chorthippus biguttulus</i>	17 spg. (probably)	8 + X	8 8 + X	—	X divides equa- tionally in 2nd	GÉRARD '09 a, '09 b
<i>Chorthippus curtipennis</i>	17 spg.	8 + X	8 8 + X	—	X divides equa- tionally in 2nd. Possibly sperma- togonal synap- sis of 6 chromo- somes	DAVIS '08 MEEK '12 LEWIS & ROBERTSON, '16, WENRICH '17
<i>Chorthippus parallelus</i>	17 spg.	—	8 8 + X	—	—	MEEK '13 b
<i>Chorthippus viridulus</i>	17 spg.	8 + X	8 8 + X	—	X divides equa- tionally in 2nd	MEEK '11
<i>Chortophaga viridifasciata</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	DAVIS '08
<i>Chortophaga</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd. Occasional sperma- togonal unions	MC CLUNG '05, '14
<i>Circotettix lobatus</i>	21 spg.	10 + X	10 10 + X	—	Supernumeraries present in some individuals	CAROTHERS '17
<i>Circotettix rabula</i>	21 spg.	10 + X	10 10 + X	—	Supernumeraries present in some individuals	CAROTHERS '17
<i>Clinoccephalid sp.?</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14
<i>Dactylotum</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14
<i>Dissosteira carolina</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	DAVIS '08
<i>Dissosteira</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14
<i>Encoptolophus sp.?</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14
<i>Eremnus</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14
<i>Hadrotettix</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14
<i>Hesperotettix brevipennis</i>	—	11 + X	—	—	Maturation normal	MC CLUNG '17
<i>Hesperotettix festivus</i>	—	11 + X	—	—	Maturation normal	MC CLUNG '17

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Hesperotettix pratensis</i>	22 (= 23) spg.	11 (= 11 + X)	11 11 (= 11 + X)	—	X divides equa- tionally in 2nd. X attached to an autosome	MC CLUNG '05, '17
<i>Hesperotettix speciosus</i>	22 (= 23) spg.	11 (= 11 + X)	11 11 (= 11 + X)	—	X divides equa- tionally in 2nd. X attached to an autosome	MC CLUNG '05, '17
<i>Hesperotettix viridis</i>	19-22 (= 23) spg.	11 + X 11 10 9 } (= 11 + X	10 (= 11 + X) 11 (= 11 + X) 11 11 + X 10 (= 11)	—	X divides equa- tionally in 2nd. X attached to an autosome	MC CLUNG '05, '17
<i>Hippiscus phoenic- opterus</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14
<i>Hippiscus tuberculatus</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	DAVIS '08
<i>Mecostethus sp.?</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14
<i>Melanoplus (Caloptenus) atlantis</i>	23 spg.	11 + X	11 11 + X	—	—	NOWLIN '12 MEEK '13 b
<i>Melanoplus bivittatus</i>	23 spg.	11 + X	11 11 + X	—	—	NOWLIN '08 MEEK '13 b
<i>Melanoplus dawsonii</i>	23 spg.	—	—	—	—	MEEK '13 b
<i>Melanoplus differentialis</i>	23 spg.	12	11 12	—	X to pole in 1st	NOWLIN '12
<i>Melanoplus femoratus</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	DAVIS '08
<i>Melanoplus femur- rubrum</i>	23 spg. 22 oog.?	12	11 12	—	X divides equa- tionally in 2nd	WILCOX '95, '96 NOWLIN '12
<i>Melanoplus packardii</i>	23 spg.	12	11 12	—	X divides equa- tionally in 2nd	NOWLIN '12 MEEK '13 b
<i>Mermiria bivittata</i>	22 (= 23) spg. 22 (= 24) ♀ soma	11 (= 11 + X)	11 11 (= 11 + X)	—	X attached to autosome in both sexes	MC CLUNG '05, '17
<i>Mermiria sp.?</i>	23 spg.	11 + X	—	—	X not attached to autosome	MC CLUNG '17
<i>Mesobryma sp.?</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	MC CLUNG '14

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Nomotettix</i> sp.?	13 spg.	—	—	—	$\sigma^0 = \text{XO}$	RAYBURN '17
<i>Oedipoda</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	BUCHNER '09
<i>Orphulella</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MCCLUNG '14
<i>Pamphagus marmoratus</i>	19 spg. 20 ♀ soma	9 + X	9 9 + X	—	X divides equationally in 2nd	GRANATA '10
<i>Paratettix ceculatus</i>	—	6 + X	—	—	X to pole in 1st	ROBERTSON '16
<i>Paratettix texanus</i>	—	6 + X	—	—	X to pole in 1st	ROBERTSON '16
<i>Paratettix</i> sp.?	13 spg.	6 + X	6 6 + X	—	X to pole in 1st	HARMAN '15, '20
<i>Paroxya</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MCCLUNG '14
<i>Philostroma</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MCCLUNG '14
<i>Phaetaliotes</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MCCLUNG '14
<i>Phrynotettix magnus</i>	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	PINNEY '08 WENRICH '16
<i>Proracorypha</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MCCLUNG '14
<i>Pseudopomala</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MCCLUNG '14
<i>Pseudotrimero-tropis caeruleipennis</i>	23 spg.	11 + X	—	—	—	KING '23
<i>Pseudotrimero-tropis cyaneipennis</i>	23 spg.	—	—	—	—	KING '23
<i>Pseudotrimero-tropis thallasica</i>	21 spg.	—	—	—	Small number possibly due to spermatogonial union	KING '23
<i>Psinidia</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MCCLUNG '14
<i>Rhomaleum</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equationally in 2nd	MCCLUNG '14
<i>Schistocerca alutacea</i>	23 spg.	12	11 12	—	$\sigma^0 = \text{XO}$	HARTMANN '18

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Schistocerca americana</i>	23 spg.	12	11 12	—	♂ = XO	HARTMANN '13
<i>Schistocerca</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	McCLUNG '14
<i>Scirtetica</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	McCLUNG '14
<i>Spharagemon</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	McCLUNG '14
<i>Stauronotus</i> <i>maroccanus</i>	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	ARTOM '09
<i>Syrbula</i> <i>aeuticornis</i>	23 spg.	11 + X	11 11 + X	—	MONTGOMERY's account probably erroneous. X divides equa- tionally in 2nd	MONTGOMERY '05 ROBERTSON '16
<i>Syrbula</i> <i>admirabilis</i>	23 spg.	11 + X	11 11 + X	—	—	ROBERTSON '08
<i>Syrbula</i> <i>fusca-vittata</i>	23 spg.	12	—	—	—	ROBERTSON '08
<i>Syrbula</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	McCLUNG '14
<i>Tettigidea parvi- pennis-pennata</i>	13 spg. 14 oog.	6 + X	—	—	—	ROBERTSON '16
<i>Tettigidea</i> <i>parvipennis</i>	13 spg. 13 ♂ soma 14 oog.	6 + X	6 6 + X	—	Supernumerary in some cases	ROBERTSON '15, '16, '17
<i>Trimerotropis</i> <i>fallax</i>	23 spg. 24 ♀ soma	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	CAROTHERS '17
<i>Trimerotropis</i> <i>suffusa</i>	23 spg. 24 ♀ soma	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	CAROTHERS '17
<i>Trimerotropis</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	McCLUNG '14
<i>Tropidolophus</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	McCLUNG '14
<i>Tryxalis</i> <i>nasuta</i>	21 spg.	10 + X	—	—	—	BRUNELLI '10, '11
<i>Tryxalis</i> sp.?	23 spg.	11 + X	11 11 + X	—	X divides equa- tionally in 2nd	McCLUNG '14
2. BLATTIDAE						
<i>Blatta germanica</i>	23 spg. 24 oog.	11 + X	11 11 + X	—	—	STEVENS '05 WASSILIEFF '07

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Leucophaea maderiae</i>	23 spg. 24 oog. 24 ♀ soma	—	11 12	—	Unpaired X to pole in 1st	MORSE '09
<i>Periplaneta americana</i>	33 spg. 34 oog. 34 ♀ soma	16 + X	16 16 + X	16 16 + X	X in ♂ closely associated with plasmosome	MOORE & ROBINSON '04 MORSE '09 HOGBEN '20
<i>Stylopyga orientalis</i>	—	—	—	—	Probably an odd X in ♂ as in other Blattidae	MORSE '09
3. GRYLLIDAE						
<i>Apithes agitator</i>	13 spg.	6 + X	—	—	—	BAUMGARTNER '16
<i>Gryllotalpa borealis</i>	23 spg. 24 oog.	12	12 11	12 11	After pseudo-reduction, 1 accessory and 1 uneven pair	PAYNE '12, '16
<i>Gryllotalpa vulgaris</i> (Bucharest)	14(+)spg., possibly 17	7	7	7	Analysis of chromosomes doubtful	VOINOV '12, '14a, '14b, '16, '25
<i>Gryllotalpa vulgaris</i> (Freiburg)	12 spg.	6	—	—	Includes 1 unequal pair	VOM RATH '92, '05 PAYNE '16
<i>Gryllotalpa vulgaris</i> (Italy?)	17 spg.	9	—	—	Unmated X to pole in 1st	SENNA '11
<i>Gryllotalpa vulgaris</i> (Naples)	15 spg.	8	—	—	After pseudo-reduction, 1 uneven pair, 1 accessory, and 1 heteromorphic pair	PAYNE '16
<i>Gryllus assimilis</i> ?	29 spg.	14 + X	14 14 + X	—	—	BAUMGARTNER '02, '04
<i>Gryllus campestris</i>	29 spg.	14 + X	14 14 + X	—	Accessory reported in ♀. Retracted according to MOHR '15	BUCHNER '09, '10
<i>Gryllus desertus</i>	21 spg.	10 + X	—	—	Unmated X to pole in 1st	BRUNELLI '09
<i>Gryllus domesticus</i>	21 spg. 21 ♂ soma 22 oog. 22 ♀ soma	10 + X	10 10 + X	—	—	GUTHHERZ '07, '08, '09 BAUMGARTNER '04 MEEK '13b
<i>Gryllus</i> sp.?	23 spg. 24 ♀ soma	12	—	—	—	BAUMGARTNER '12

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
4. LOCUSTIDAE						
<i>Anabrus</i> sp.?	33 spg.	16 + X	16 16 + X	—	X divides equa- tionally in 2nd. X is united with an autosome te- trad during meiosis	MC CLUNG '02, '05, '14
<i>Ceuthophilus</i> <i>latebricola</i>	37—39 spg.	—	—	—	X to pole in first	THOMPSON '11
<i>Ceuthophilus</i> sp.?	37 spg. (probably)	18 + X	18 18 + X	—	Supernumeraries present in varia- ble number	STEVENS '12
<i>Conocephalus</i> sp.?	33 spg.	—	—	—	—	MC CLUNG '14
<i>Decticus</i> <i>verrucivorus</i>	23 spg.	11 + X	11 11 + X	11 11 + X	—	VEJDOWSKY '12
<i>Decticus</i> <i>verrucosus</i>	31 spg.	—	—	—	—	BUCHNER '09
<i>Diestrammena</i> <i>marmorata</i>	57 spg.	28 + X	28 28 + X	—	X to pole in 1st	SCHELLEN- BERG '13
<i>Jamaicana</i> <i>flava</i>	35 spg.	17 + X	17 17 + X	—	X divides equa- tionally in 2nd	WOOLSEY '15
<i>Jamaicana</i> <i>subguttata</i>	35 spg.	17 + X	17 17 + X	—	1 individual showed two auto- somes fused. X divides equa- tionally in 2nd	WOOLSEY '15
<i>Jamaicana</i> <i>unicolor</i>	35 spg.	17 + X	—	—	Some individuals showed certain autosomes fused	WOOLSEY '15
<i>Leptophyes</i> <i>punctatissima</i>	31 spg. 31♂ soma 32 oog. 32♀ soma	—	—	—	X to pole in 1st	MOHR '15
<i>Locusta</i> <i>viridissima</i>	29 spg. 29♂ soma 30 oog. 30♀ soma	14 + X	14 14 + X	—	X divides equa- tionally in 2nd. OTTE gives 33 spg.	OTTE '06, '07 MOHR '16
<i>Microcentrum</i> sp.?	33 spg.	16 + X	16 16 + X	—	X divides equa- tionally in 2nd	MC CLUNG '02
<i>Orchesticus</i> sp.?	33 spg.	16 + X	16 16 + X	—	X divides equa- tionally in 2nd	MC CLUNG '02, '14
<i>Orchelimum</i> <i>vulgaris</i>	33 spg. 34 oog. neither count certain	—	—	—	♂ = XO. ♀ = 2X. X very large	KING '24

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Orchelimum concinnum</i>	33 spg. 34 oog. neither count certain	—	—	—	$\sigma = X0$ . $\varphi = 2X$ . X very large	KING '24
<i>Orphania denticauda</i>	31 spg.	15 + X	15 15 + X	—	X divides equationally in 2nd	DE SINETY '01
<i>Platycleis grisea</i>	—	—	—	—	X to pole in 1st and equationally in 2nd	DE SINETY '01
<i>Scudderia</i> sp.?	33 spg.	16 + X	16 16 + X	—	X divides equationally in 2nd	MC CLUNG '02, '14
<i>Steiroxys trilineata</i>	29 spg. 29 ♂ soma	14 + X	14 14 + X	—	X divides equationally in 2nd	DAVIS '08 MEEK '13b
<i>Stenopelmatus</i> sp.?	47 spg.	—	23 23 + X	—	'05 account has erroneous chromosome counts	STEVENS '05, '09
<i>Ziphidium fasciatum</i>	—	—	—	—	Identified X chromosome in ♂	MC CLUNG '99
<i>Ziphidium</i> sp.?	33 spg. (probably)	16 + X	16 16 + X	—	X divides equationally in 2nd	MC CLUNG '99, '01, '02, '08, '14
5. MANTIDAE						OGUMA '21
<i>Paratenodera aridifolia</i>	27 spg. 28 ♀ soma	12 + X <sup>I</sup> X <sup>II</sup> Y	12 + X <sup>I</sup> + X <sup>II</sup> 12 + Y	—	$\varphi = 2X^I + 2X^{II}$	
<i>Tenodera superstitionis</i>	27 spg. 28 ♀ soma	12 + X <sup>I</sup> X <sup>II</sup> Y	12 + X <sup>I</sup> + X <sup>II</sup> 12 + Y	—	$\varphi = 2X^I + 2X^{II}$	OGUMA '21
6. PHASMIDAE						
<i>Aplopus mayeri</i>	35 spg.	17 + X	17 17 + X	—	X divides equationally in 2nd	JORDAN '08a, '08b
<i>Leptynia attenuata</i>	36 (= 37) spg. 36 (= 38) oog.	18 (= 18 + X)	18 18 (= 18 + X)	—	X attached to an autosome	DE SINETY '01
<i>Menexenus obtusospinosus</i>	—	—	—	—	Probably has X attached to an autosome in ♂	DE SINETY '01
<i>Dixippus morosus</i>	60 oog. (+)	28 (+) 62-64 ♀	—	—	DE SINETY suggests X attached to an autosome	DE SINETY '01 PEHANI '25

the Y remains compact. In the division both components of the X pass to the same pole while the Y goes to the pole opposite. In the second division all sex chromosomes divide equationally. Since the autosomes divide normally in both divisions, it is clear that 2 types of sperms must be formed, one with  $X^I + X^{II}$ , the other carrying the Y. The diploid set of chromosomes as seen in the female clearly includes no Y, but  $2X^I + 2X^{II}$ , so that the main course of the chromosome cycle seems clear.

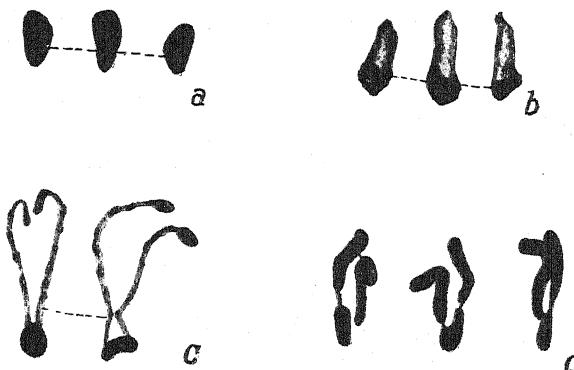


Fig. 21. *Tenodera superstitionis* (OGUMA, 21)—a, b, c & d Successive stages in the behavior of the sex chromosomes of the first spermatocyte. The two components of the X are more diffuse than the Y.

*Phasmidae*: According to JORDAN ('08a, '08b) the males of *Aplopus* have the XO condition, with segregation occurring in the first spermatocyte division. Attachments between the X and an autosome were reported in the males of several other species of the family (DE SINETY, '01), these being the first cases in which such association was discovered. The chromosome numbers seem to be quite high in most cases and as PEHANI ('25) has recently shown, accurate counts are often almost impossible.

#### DERMAPTERA

RANDOLPH ('08) reported an XY pair in the males of *Anisolabis*, resting her claim on the fact that there is a chromatin nucleolus in the growth stage and that one pair of chromosomes lags on the first spermatocyte spindle. The work done by other investigators in this order has been centered on the single species *Forficula auricularia*. ZWEIGER ('06a & b) was astonished to find that the number of chromosomes in spermatogonial cells is variable, some carrying 24 and others 26, both numbers occurring in different cysts of a single testis. In the first spermatocyte there are 12, 13, or 14 chromosome bodies, and anaphases show 1 or 2 lagging chromosomes. The same numbers are found in the second division. ZWEIGER did not hesitate to identify the chromosomes responsible for these numerical variations as sex chromosomes and therewith arrived at the generalization that sex chromosomes

can be of no significance in sex determination but rather represent chromosomes that are rudimentary or degenerating. STEVENS ('10) working on the same species described an unequal pair of chromosomes the members of which separate and pass to opposite poles in the first division, whereas the second division is equational. This evidence thus indicated an XY pair in the male, but it is to be noted that Miss STEVENS also reported some variation in the number of elements in the first spermatocytes (11, 12 & 13). MEEK'S work ('13a, '13b, '15) threw no further light on this aspect, but PAYNE ('14) took up the question with a view of investigating the chromosomal variations. Unlike STEVENS he hesitated to identify the XY pair, but confirmed fully the previous reports on the variations in the chromosome numbers. According to PAYNE the most probable explanation for the different numbers observed lies in the failure of some of the chromosomes to pair in the first spermatocyte. Thus the number 13 really represents 11 tetrads and 2 univalent chromosomes that have failed to conjugate. PAYNE's interpretation receives support from his figures, but it seems certain that it is not applicable to all variations observed in the species. He himself reported spermatogonial numbers (where no pairing can be involved) varying from 24 to 27, not to mention two oogonial counts of 25, and the most natural conclusion seems to be that there are additional complications due to supernumerary chromosomes. Unfortunately nothing definite on their behavior in the meiotic growth stages has been reported, the evidence on the nucleoli present during that time being confusing.

## DERMAPTERA

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Anisolabis maritima</i>	24 spg. 24 oog. 24 ♀ soma	12	12	12	XY distinguishable only in growth stages and because of lagging	RANDOLPH '08
<i>Forficula auricularia</i>	24-27 spg. 25 oog. (not certain)	12-14	11-14	10-14	Probably XY to opposite poles in 1st. Variation in numbers possibly due to failure of some chromosomes to pair	MEEK '13a, '13b, '15 PAYNE '14 ZWEIGER '06a, '06b STEVENS '10

## NEUROPTERA (Corrodentia, Odonata, Plecoptera, Trichoptera)

For the sake of convenience, the orders which were formerly included in the one large group of Neuroptera are here taken up together. In a measure their diversity is reflected in the conditions observed in the sex chromosomes.

Already in 1901, McCLEUNG stated that he had found an accessory chromosome in the Neuroptera, but neither this remark nor a similar one made later by BUCHNER ('09) was elaborated by these two authors. For the rest, the various accounts may be summed up as follows: In both the *Corrodentia* and the *Odonata*, the simple XO condition seems to obtain in the males. But only in the last named order has a study of female as well as male cells made a demonstration of this condition more or less complete (in *Anax*, LEFEVRE & MCGILL, '08). Among the *Trichoptera*, LUTMAN ('10) has reported precocious condensation in one of the tetrads of the first spermatocyte division, but his description permits of no definite interpretation in regard to the nature of the chromosome or chromosomes concerned. In the *Plecoptera*

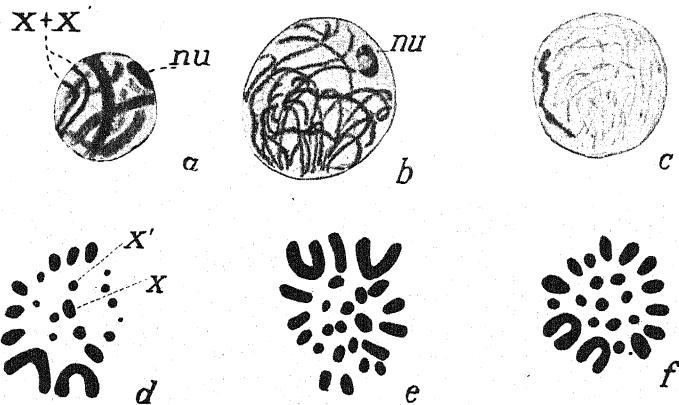


Fig. 22. *Perla marginata* (JUNKER, '23) — a Leptotene stage of first spermatocyte ( $X$  and  $X'$  = components of compound sex chromosome). b Leptotene stage in "male oocyte", no heteropycnotic being in evidence. c Leptotene stage in oocyte of female. True nucleolus shown. d Spermatogonial metaphase. e Oogonial metaphase. f Metaphase of "male oogonium".

some very interesting conditions are found. NAKAHARA ('19) reported an XY in the male of *Perla immarginata*, and although he did not check his findings by a study of the conditions in the female, his conclusion receives every possible support from the spermatogenesis. Peculiarly enough, in a species closely related to the form studied by NAKAHARA, the general organization as well as the chromosomal conditions are quite different (fig. 22). The form in question is *Perla marginata* where it has been known for some time that males show an ovary-like structure connected with the testis. In 1923 JUNKER showed that the spermatogenesis has the following course: Spermatogonia contain 22 chromosomes, all but 2 of which can evidently be arranged in pairs. In the preparatory stages of the spermatocytes, 2 unequal chromatin nucleoli form 2 threads that are shorter and stain more intensely than the autosomal threads. A slight tendency toward pairing is noticeable in these 2 threads, but in the metaphase plate they have condensed to form 2 separated chromosomes, whereas the autosomes have paired to form 10 tetrads.

The heterochromosomes do not divide in the first division and both pass to the same pole, while in the second division they divide equationally. Since the autosomal tetrads divide normally, it is plain that sperms with 10 and 12 chromosomes are formed and that the male has an unmated compound X, i. e.  $X^I X^{II} O$ .

The oogenesis bears this out. The diploid number in the female is 24. These conjugate normally in the preparatory phases of the meiotic divisions and no trace of a heteropycnotosis is observable. As might be expected from the study of the male then, the female's sex chromosomes comprise 2 compound X chromosomes,  $X^I X^{II} + X^I X^{II}$ . A remarkable feature is embodied in the behavior of the sex chromosomes of the ovary-like structures (the "male ovary") of the male. Although the cells there have the typical male chromosome complex, i. e. 22 chromosomes, the 2 unequal components of the compound X form long threads like the autosomes. This occurs despite the fact that neither of them has a mate and therefore cannot undergo a synaptic stage like the paired autosomes.

Conditions in the *Isoptera* are unfortunately unfavorable to cytological analysis. STEVENS ('05) could find no sex chromosomes in *Termopsis angusticollis* males. It is to be hoped that some of the tropical species will be investigated and that thereby some light may be thrown on the origin of the different castes.

#### NEUROPTERA

Species	Diploid Chromo-some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Anax junius</i>	28 ♀ soma 27 spg.	13 + X	13 + X	13 13 + X	—	LEFEVRE & MCGILL '08 MCGILL '04 SMITH '16
<i>Cerastipsocus venosus</i>	17 spg.	8 + X	8 8 + X	—	2nd division probably equa-tional for X	BORING '13
<i>Libellula basalis</i>	25 spg.	12 + X	12 12 + X	12 12 + X	—	SMITH '16
<i>Perla immarginata</i>	10 spg.	4 + XY	4 + X 4 + Y	4 + X 4 + Y	—	NAKAHARA '19
<i>Perla marginata</i>	24 oog. 22 spg. 22 ♂ ovary	10 + X <sup>I</sup> + X <sup>II</sup>	10 + X <sup>I</sup> + X <sup>II</sup> 10	10 + X <sup>I</sup> + X <sup>II</sup> 10	Sex chromo-somes in female 2 X <sup>I</sup> + 2 X <sup>II</sup>	JUNKER '23
<i>Platyphyllax designatus</i>	55—60 oog.	30	80	—	One tetrad con-denses in advance of the others, possibly an XY	LUTMAN '10
<i>Sympetrum semicircumatum</i>	25 spg.	12 + X	12 + X	12 12 + X	—	SMITH '16

## COLEOPTERA

HENKING suggested in 1892 that a small chromatin nucleolus present in the male germ cells of *Agelastica alni* may be similar in nature to a like body that he had already found in the hemipteran *Pyrrhocoris* and which, as we now know undoubtedly represented the sex chromosome. In 1902 PROWAZEK noticed that a large number of first spermatocyte divisions in *Oryctes* showed a peculiarly formed chromosome that lagged on the spindle. Despite the fact that he suggested that two kinds of sperms might be produced in this beetle, PROWAZEK was several steps removed from recognizing the true mechanism of the distribution of sex chromosomes and their true significance. HOLMGREN's conclusions ('01, '02) that two kinds of sperms are produced in *Staphylinus* and *Silpha* were based chiefly on differences that he believed to have observed in the spermatogonia and not at all on a recognition of the sex chromosomes. VOINOV in 1903 described as an accessory chromosome in *Cybister* a body which is divided in both spermatocyte divisions and finally assumes an extranuclear position in the spermatid. It is possible that he really was dealing with an XY pair, but in that case it is not likely that the extranuclear body of the spermatids was traced correctly. All in all, no definite conclusion is possible about these earlier investigations, and it was not until 1905 when Miss STEVENS published her first paper on chromosomes in *Tenebrio* that sex chromosomes were definitely described and recognized as such in this group.

In the great majority of the large number of cases where sex chromosomes have been described in Coleoptera since 1905, no complete analysis has been made. Very often the conclusion that sex chromosomes are present has been based on an examination of metaphase plates of the first spermatocytes only. In some cases the identification of the material worked on was incomplete or inaccurate and Miss STEVENS' own work on beetles is not above criticism in this regard. A certain amount of confusion as to the details in regard to the sex chromosomes in this order is largely attributable to superficial work of this kind.

GOLDSMITH ('19) has grouped sex chromosomes as they occur in Coleoptera under three headings. In elaborating the general status of the question, a similar grouping will be followed there:

a) The XO condition has been described in the males of a number of widely separated species. The X goes undivided to one pole in the first spermatocyte division in every case except one, this exception being *Photinus pennsylvanicus*. The latter reverses the usual sequence, the X dividing equationally in the first and going undivided to one pole in the second spermatocyte division.

b) The XY condition is the one most commonly observed in the male beetles. In every case except *Haltica* this unequal pair of sex chromosomes fuses and appears more or less as a single body on the spindle of the first spermatocyte division. However, the members of the pair always separate at this time and go to opposite poles. The second division then is always equational for them. The few cases in which the female chromosomes have been studied seem to show that the X is always the larger member of the unequal pair.

c) The presence in the male of a compound X of 2 components has been described in *Cicindela* (GOLDSMITH, '19) and *Leptinotarsa* (WIEMAN, '10). (It should however be mentioned that STEVENS ('06) had previously reported both of these cases as simple XY types.). It is not certain whether *Dytiscus marginalis* also has an X of two components. The fact that the oogonial number has been reported as 40 (HENDERSON, '07; DEBAISIEUX, '09) and the spermatogonial as 38 would speak for such an interpretation, but the account of SCHÄFER ('07) according to which the sex chromosome complex divides in both spermatocyte divisions, suggests an XY pair.

In this connection should be mentioned the interesting case of *Blaps* (fig. 23 and 24). In the interpretation given by NONIDEZ ('14, '15, '20) the male has sex chromosomes of the XO type, but there is a compli-

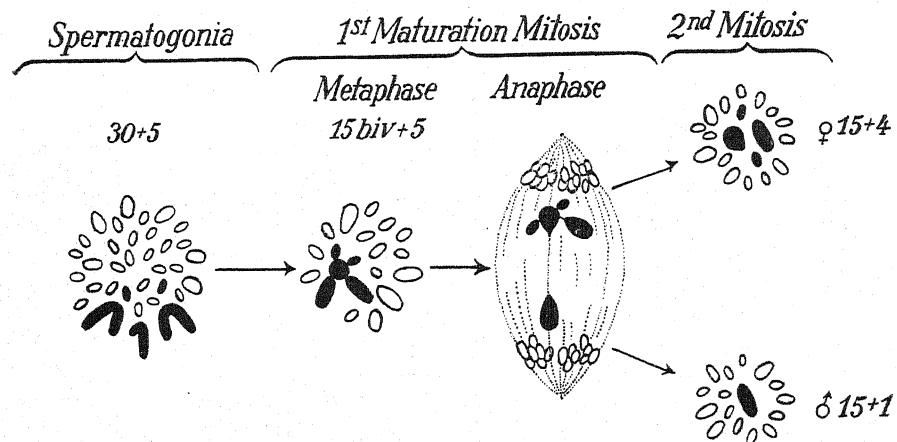


Fig. 23. *Blaps lusitanica* (NONIDEZ, '20)—Diagram of the behavior of the sex chromosomes in the spermatogenesis.

cation due to the fact that 4 autosomes are associated with the X during the preparatory phases and up to the first division. Following the last spermatogonial division, the chromosome regarded as the X forms a long thread but condenses rapidly thereafter. The associated chromosomes behave more like the true autosomes, but although they form long threads like the latter they do not undergo pairing. In the division, the X and 3 of its associated chromosomes go to one pole while the remaining member of this peculiar complex goes to the opposite pole (fig. 23). In contrast to this view WILSON ('25) preferred to regard the case as one in which a compound X of 4 components is associated with a large Y. Such an interpretation would seem to be a more natural one in view of the fact that one large chromosome (WILSON's Y) always goes to the pole opposite to that which receives the remaining 4 heterochromosomes. But the point can not be settled without an investigation of the chromosomes of the female.

The possibility of heteropycnotosis in the case of maturation in the female has been brought out in two cases. WIEMAN described a bi-

## COLEOPTERA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Adalia bipunctata</i>	20 spg.	9 + XY	9 + X 9 + Y	—	—	STEVENS '06
<i>Agelastica alni</i>	24 spg.	16 or 17	—	—	Chromatin nucleolus in 1st cyte	HENKING '92
<i>Anomoglossus emarginatus</i>	—	18 + X	18 18 + X	18 + X	—	STEVENS '06
<i>Blepharida rhois</i>	—	15 + XY	15 + X 15 + Y	15 + X 15 + Y	—	STEVENS '06
<i>Blaps lusitanica</i>	35 spg.	19 + X	16 18 + X	—	WILSON thinks male X <sup>I</sup> X <sup>II</sup> X <sup>III</sup> X <sup>IV</sup> Y. Behavior of two small chromosomes slightly variable	NONIDEZ '11, '15, '20 WILSON '25 a
<i>Blaps walshi</i>	34 spg.	18 + X	16 17 + X	—	Behavior of two small chromosomes slightly variable	NONIDEZ '15
<i>Cicindela primeriana</i>	20 spg.	9 + XY	9 + X 9 + Y	—	STEVENS states spg. = 18, but her figures show 20. Trilobed XY pair (GOLDSMITH thinks 2 X)	STEVENS '06
<i>Cicindela sexguttata</i>	24 oog. 22 spg.	10 + X <sup>I</sup> X <sup>II</sup>	10 10 + X <sup>I</sup> + X <sup>II</sup>	—	Bilobed chromatin nucleolus in the prophases of both oocytes and spermatoocytes	GOLDSMITH '19
<i>Cicindela vulgaris</i>	22 spg.	—	—	—	Trilobed XY pair (see GOLDSMITH '19)	STEVENS '09
<i>Chelymorpha argus</i>	22♀ soma 22 spg.	10 + XY	10 + X 10 + Y	—	—	STEVENS '06
<i>Chalenius aestivus</i>	—	17	—	—	XY to pole in 1st	STEVENS '06
<i>Chalenius pennsylvanicus</i>	—	10	--	—	XY to pole in 1st	STEVENS '06
<i>Chrysocanus auratus</i>	—	13	—	—	XY pair present	STEVENS '09

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Chrysomela similis</i>	28 spg.	11 + X 11 + X	11 11 + X	11 11 + X	—	STEVENS '09
<i>Coccinellidae</i> (a no. of species)	20 spg.	10	10	—	—	STEVENS '09
<i>Colymbetes fuscus</i>	—	—	—	—	Reports no heterochromosome in oogenesis	GÜNTHERT '10
<i>Coptocycla aurichalcea</i>	22 spg.	10 + XY 10 + Y	10 + X 10 + Y	10 + X 10 + Y	—	NOWLIN '06
<i>Coptocycla clavata</i>	18 spg.	—	—	—	XY present	STEVENS '09
<i>Coptocycla guttata</i>	18 spg.	8 + XY 8 + Y	8 + X 8 + Y	8 + X 8 + Y	—	NOWLIN '06
<i>Cotalpa lanigera</i>	20 spg.	9 + XY 9 + Y	9 + X 9 + Y	9 + X 9 + Y	—	SHAFFER '20
<i>Oylene robinia</i>	20 spg.	9 + XY	—	—	XY to poles in 1st, probably	STEVENS '09
<i>Diabrotica 12-punctata</i>	19 spg.	9 + X	9 9 + X	9 9 + X	Supernumeraries may increase no. of chromosomes	HOY '14
<i>Diabrotica soror</i>	19 spg.	9 + X	9 9 + X	9 9 + X	Slightly variable no. of supernumeraries	STEVENS '08
<i>Diabrotica vittata</i>	22 soma 21 soma 21 spg.	10 + X 11	10 10 + X	10 10 + X 11	HOY finds two kinds of embryos, with 21 and 22 chromosomes in somatic cells	STEVENS '08 HOY '14, '18
<i>Doryphora clivicola</i>	—	16 + XY 16 + Y	16 + X 16 + Y	—	XY to poles in 1st	STEVENS '09
<i>Doryphora decimlineata</i>	36 spg.	17 + XY	17 + X 17 + Y	—	This genus called <i>Leptinotarsa</i> by WIEMAN '10	STEVENS '06 WIEMAN '10
<i>Dytiscus circum-cinctus</i>	38 spg.	19	19	19	Reports 2 accessories. (Possibly an XY pair)	SCHÄFER '07
<i>Dytiscus marginalis</i>	40 oog. 38 spg.	19	19	19	SCHÄFER reports 2 accessories. (Possibly an XY pair.) HENDERSON '07 could find no accessory	SCHÄFER '07 HENDERSON '07 DEBAISIEUX '09
<i>Elater sp.? 1</i>	20 oog. 19 spg.	9 + X	—	—	X to pole in 1st	STEVENS '06
<i>Elater sp.? 2</i>	19 spg.	9 + X	—	—	X to pole in 1st	STEVENS '06

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Ellychnia corrusca</i>	19 spg.	—	—	—	Unpaired X	STEVENS '06
<i>Epicauta cinerea</i>	20 spg.	9 + XY 9 + Y	9 + X 9 + Y	—	—	STEVENS '09
<i>Epicauta penn- sylvanica</i>	20 spg.	9 + XY	9 + X 9 + Y	—	—	STEVENS '09
<i>Epilachna borealis</i>	18♂ soma 18 spg.	8 + XY	8 + X 8 + Y	—	Hoy finds two kinds of embryos, XY and XX	STEVENS '06 HOY '18
<i>Euchroma gigantea</i>	—	12 + XY	—	—	XY to poles in 1st	NICHOLS '10
<i>Euphorbia indica</i>	20 spg.	9 + XY	9 + X 9 + Y	9 + X 9 + Y	—	STEVENS '06
<i>Galerita bicolor</i>	30 spg.	—	—	—	XY pair present	STEVENS '06
<i>Haltica chalybea</i>	22 spg.	10 + XY	10 + X 10 + Y	—	—	STEVENS '09
<i>Hydrophilus piceus</i>	30 spg.	15	15	—	Chromatin nucle- olus in 1st cyte not accessory	ARNOLD '08
<i>Lachnostenus delata</i>	20 spg.	9 + XY	9 + X 9 + Y	9 + X 9 + Y	—	SHAFFER '20
<i>Lachnostenus fusca</i>	20 spg.	9 + XY	9 + X 9 + Y	9 + X 9 + Y	—	SHAFFER '20
<i>Lachnostenus gracilis</i>	20 spg.	9 + XY	9 + X 9 + Y	9 + X 9 + Y	—	SHAFFER '20
<i>Lachnostenus tristis</i>	20 spg.	9 + XY	9 + X 9 + Y	9 + X 9 + Y	—	SHAFFER '20
<i>Lema trilineata</i>	32 spg.	15 + X 15 + Y	—	—	—	STEVENS '09
<i>Leptinotarsa decemlineata</i>	—	—	—	—	WIEMAN thinks X <sup>I</sup> X <sup>II</sup> , STEVENS XY	STEVENS '06 WIEMAN '10
<i>Leptinotarsa signaticollis</i>	—	17	17 16	—	X <sup>I</sup> X <sup>II</sup> acting as unit until an- aphase of 2nd?	WIEMAN '10
<i>Limoneus griseus</i>	17 spg.	8 + X	8 8 + X	8 8 + X	—	STEVENS '09
<i>Lina laponica</i>	—	17	—	—	XY probably to poles in 1st	STEVENS '09
<i>Listotrophus cingulatus</i>	26 spg.	12 + XY	12 + X 12 + Y	—	—	STEVENS '09
<i>Necrophorus sayi</i>	13 spg.	6 + X	6 6 + X	6 6 + X	—	STEVENS '09

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Obera tripunctata</i>	—	—	—	—	XY pair present	STEVENS '09
<i>Odontota dorsalis</i>	16 spg.	7 + XY	7 + X 7 + Y	—	—	STEVENS '06
<i>Oryctes nasicornis</i>	12 spg.	6	6	6	Oddly formed chromosome lags in 1st division in 10% of cases	PROWAZEK '02
<i>Passalus cornutus</i>	26 spg. (probably)	18	—	—	XY to poles in 1st, but no figures given	SHAFFER '17
<i>Pelidonata punctata</i>	20 spg.	9 + XY	9 + X 9 + Y	9 + X 9 + Y	—	SHAFFER '20
<i>Pentha obliquata</i>	16 spg.	—	7 + X 7 + Y	—	—	STEVENS '09
<i>Photinus consanguineus</i>	20 oog. 19 spg.	9 + X	9 + Y	9 9 + X	X to pole in 2nd	STEVENS '09
<i>Photinus pennsylvanicus</i>	20 oog. 19 spg.	9 + X	9 9 + X	9 9 + X	—	STEVENS '09
<i>Phytonomus punctata</i>	—	—	—	—	XY present	STEVENS '09
Rove beetle ( <i>Staphylinus</i> ?)	28 spg.	14	14	—	—	STEVENS '09
<i>Silpha americana</i>	40 spg.	19 + XY	19 + X 19 + Y	—	—	STEVENS '06
<i>Silpha carinata</i>	32 spg.	16	16	16	Probably two kinds of sperm	HOLMGREN '02
Spruce borer? (2 species?)	—	9 + XY	9 + X 9 + Y	—	Sometimes 11 in 1st cyte. May be another species	STEVENS '06
<i>Staphylinus</i> sp.?	—	—	—	—	Probably two kinds of sperm	HOLMGREN '01
<i>Tenebrio molitor</i>	20♀ soma 20 spg.	9 + XY	9 + X 9 + Y	9 + X 9 + Y	—	STEVENS '05
<i>Tetraopes tetraophthalmus</i>	20 spg.	9 + XY	9 + X 9 + Y	—	—	STEVENS '09
<i>Trirhabda canadense</i>	30♀ soma 30 spg.	14 + XY	14 + X 14 + Y	—	—	STEVENS '06
<i>Trirhabda virgata</i>	28♀ soma 28 spg.	18 + XY	13 + X 13 + Y	—	—	STEVENS '06

partite body in the preparatory phases of both sexes of *Leptinotarsa*. Its identity with sex chromosomes was however not demonstrated by tracing it through all the stages. In the same way GOLDSMITH ('19) failed to give conclusive evidence that the 2 bodies traceable through the growth stages of the oocytes in *Cicindela* represent as he thinks the four sex chromosomes fused in pairs. Nevertheless both cases merit consideration and renewed investigation.

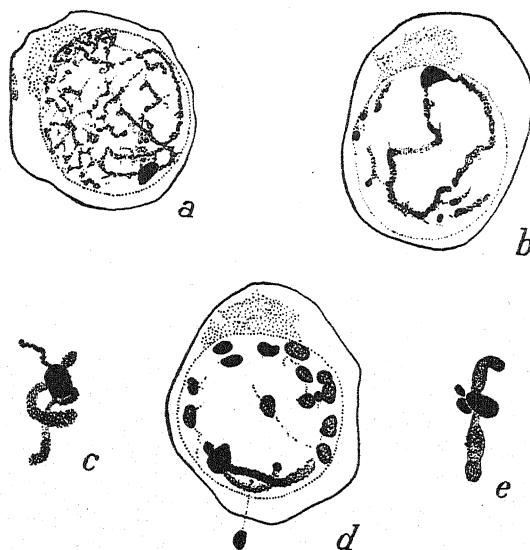


Fig. 24. *Blaps lusitanica* (NONIDEZ, '20) — a Leptotene stage of first spermatocyte, showing condensed X with attached heterochromosome threads. b Pachytene stage. c X complex in prophase of first spermatocyte. d Prophase stage. e X complex in metaphase of first spermatocyte.

#### STREPSIPTERA

HUGHES-SCHRADER ('24) described two lagging chromosomes in the first spermatocyte division of *Acroschismus wheeleri*. They may represent an XY pair, but this is of course not certain.

#### STREPSIPTERA

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Acroschismus wheeleri</i>	16 oog. 16 spg. 16 clv.	8 8 ♀	8 8 ♀	8 8 ♀	Possibly XY in males	HUGHES-SCHRADER '24

## DIPTERA

Freely admitting that the Diptera as a whole furnish material that is rather unfavorable to cytological investigation, it nevertheless seems strange that so little thorough work of this character has been done in the group.

Apparently the meiotic preparatory phases in the males of many species show some exceptional features. Thus there is reason to suspect that the synaptic stages as found in other animals are greatly modified or do not occur in many flies (KEUNECKE, '24, METZ, '22, METZ & NONIDEZ, '21, '23). If it is admitted that the genetic phenomenon of crossing over occurs at this stage, such an observation would of course help toward an explanation of the fact that in the male of *Drosophila* no crossing over has yet been observed. However, until the meiosis of the female has been adequately worked out, the significance of these cytological observations can not be evaluated.

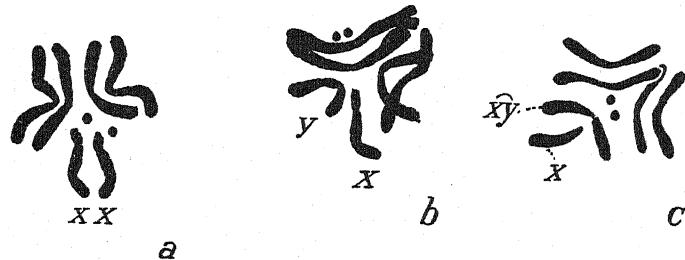


Fig. 25. *Drosophila melanogaster* (Originals of a & b from Dr. C. B. BRIDGES)—a Metaphase of oogonial division. b Spermatogonial division. c (STERN, '26 b) Oogonial metaphase showing multiple formed by an X and a Y.

In nearly all cases where sex chromosomes have been observed the male shows the XY condition (fig. 25). In two cases only (*Tephritis* and *Dasyllis*) has the XO condition been found, and in the first named of these two forms it is the second spermatocyte division that is reductional for the sex chromosome. In *Dasyllis* as well as in the numerous males with an XY pair, the first division is reductional for the chromosomes in question.

The behavior of the sex chromosomes during the preparatory stages of meiosis is known only in general outline (fig. 26). Apparently they tend to remain condensed throughout, but they have not always been clearly distinguished from nuclear inclusions like the plasmosomes. Thus STEVENS ('08) concluded that not only the XY but also a pair of small autosomes — her m chromosomes — remain condensed during the early stages in *Lucilia* and *Eristalis*. KEUNECKE (24) working on *Lucilia* could not confirm this observation. He as well as METZ ('22) have described confusing elements which are certainly not sex chromosomes, and while KEUNECKE made no attempt to trace their later history in detail, METZ's study of the large nucleolus attached to one of the autosomes in *Dasyllis* convinced him that this body partakes of the nature of a chromomere vesicle such as has been described in several Orth-

optera (CAROTHERS, '13; WENRICH, '17). True chromosome nucleoli are however often formed by the XY pair, each sex chromosome forming a separate chromosome nucleolus, or more commonly, both together forming a single nucleolus of this type — and generally this shape is maintained through the preparatory phases and up to the time of the first spermatocyte division<sup>1</sup>.

It has been the tendency of the earlier investigators to regard the larger member of the XY pair as the X chromosome. In several cases where the 2 chromosomes do not differ very much in size, this is not a safe assumption, for even when the chromosomes of the female can be studied it is often difficult to decide which member of the sex chromosome pair as seen in the male is represented twice in the female.

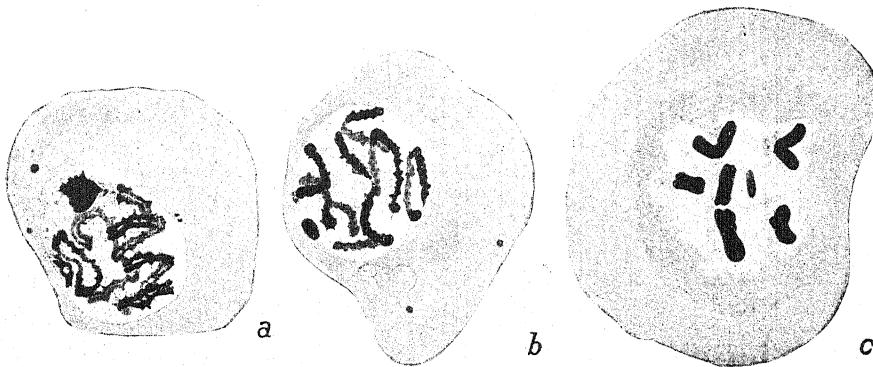


Fig. 26. *Asilus notatus* (METZ & NONIDEZ, '23) — *a* Diplotene stage with chromatin nucleolus in first spermatocyte. *b* Six bivalents and XY pair derived from chromatin nucleolus in first spermatocyte. *c* First spermatocyte metaphase. The XY bivalent constituting the smallest member.

Indeed, that the larger member is not necessarily the X is shown in *Drosophila melanogaster* where the Y seems to be slightly longer than the X.

In one form, *Anopheles punctipennis* (fig. 10) a definite and morphological association between the sex chromosomes and certain autosomes has been described (STEVENS, '11). In the resting and preparatory phases of the spermatogonial divisions the associated chromosomes appear in no discernible way to be affected by each other. The small sex chromosomes remain condensed while the attached autosomes become diffuse and behave like any normal and free autosome. When condensed each of the 2 autosomes concerned still shows a delicate thread connecting it with one of the sex chromosomes, and in the following division the 2 chromosomes thus connected always act as a unit. In the spermatocytes, these features do not appear so strikingly. In the related form, *Culex pipiens*, WHITING ('17) has described a diffuse body attached to one of the spermatogonial autosomes but does not believe that the

<sup>1</sup> A recently published study of the spermatogenesis in several species of *Drosophila* (METZ, '26) throws additional light on these questions.

evidence for regarding this body as a heterochromosome of any kind is at all conclusive.

The peculiar process observed by KEUNECKE in the spermatogonial and spermatocyte cells of certain forms (*Tephritis*, *Calliphora*, *Scatophaga*) through which certain of the autosomes fragment in a definite way, apparently never occurs in the sex chromosomes. However in view of

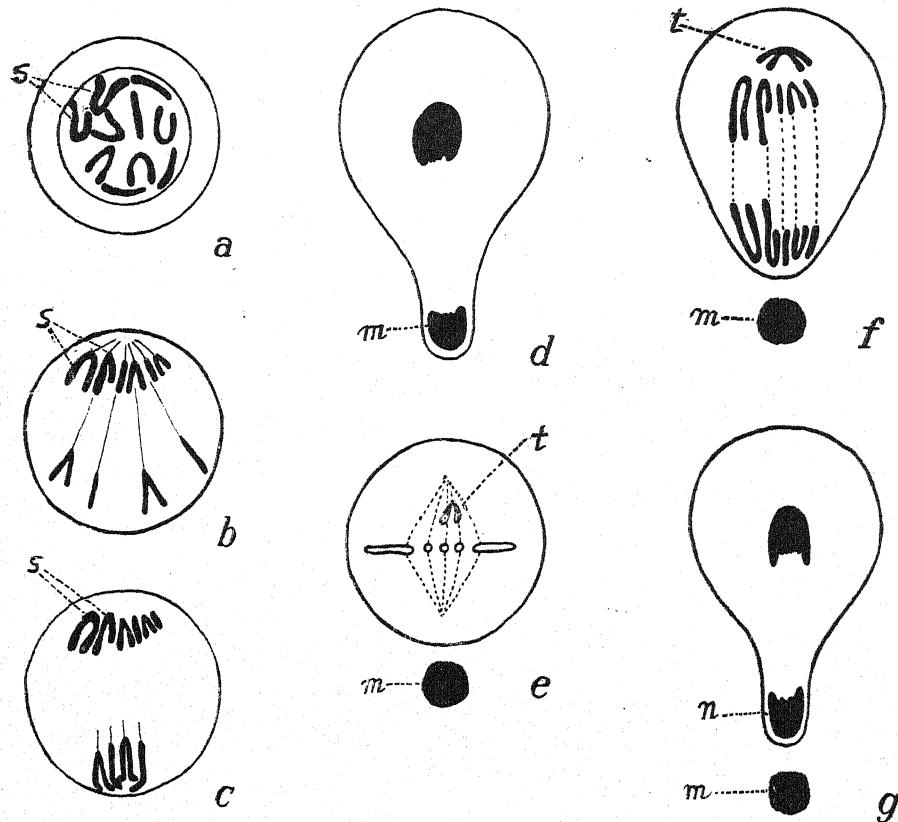


Fig. 27. *Sciara* (Original from Dr. C. W. METZ) — Diagram of chromosome behavior in the meiosis of the male. *a* Prophase of first spermatocyte. *b* & *c* Anaphases. *d* Telophase, showing inner group in bud. *e* Metaphase of second spermatocyte. *f* Anaphase of second spermatocyte. *g* Telophase of second spermatocyte; showing inner group in bud, with bud of first division still showing (*m* = degenerating group of first division). *n* = degenerating group of second division. *s* = large chromosomes going to one pole in first. *t* = smaller split chromosome going to one pole in second).

the fact that not all autosomes are subject to such fragmentation, its omission in the case of sex chromosomes may have no special significance.

The most puzzling conditions are however shown in *Sciara* (fig. 27), of which METZ has given two preliminary accounts ('25, '26). The diploid numbers of the female and male are 8 and 10 respectively. The 2 largest chromosomes as seen in the male are not present in the female (i. e. they are sex limited). No trace of synaptic stages or pseudo-reduction could be found in the spermatogenesis although the 2 largest

## DIPTERA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Anopheles punctipennis</i>	6 spg. 6 oog.	3	3	—	X and Y attached to autosomes, and these to op- posite poles in 1st, then divide equationally in 2nd	STEVENS '11
<i>Anopheles</i> sp.	—	6	6	—	Possibly an XY present	STEVENS '11
<i>Anthrax sinuosa</i>	18 spg.	—	8 + X 8 + Y	—	—	METZ '16 a
<i>Asilus notatus</i>	14 spg.	6 + XY	6 + X 6 + Y	6 + X 6 + Y	—	METZ '16 a METZ & NONIDEZ '23
<i>Asilus sericeus</i>	10 spg.	4 + XY	4 + X 4 + Y	—	—	METZ & NONIDEZ '21
<i>Calliphora erythrocephala</i>	12 oog. 12 spg.	5 + XY	5 + X 5 + Y	—	Sex chro- mosomes divide equationally in 2nd	METZ '16 a KEUNECKE '24
<i>Calliphora vomitoria</i>	12 oog. 12 spg.	5 + XY	5 + X 5 + Y	—	Sex chro- mosomes divide equationally in 2nd	STEVENS '08
<i>Culex pipiens</i>	6 spg.	3	3	3	Diffuse body attached to one autosome, possibly sex chromosome	WHITING '17
<i>Dasyllis grossa</i>	10 oog. 9 spg.	4 + X	4 4 + X	—	X divides equa- tionally in 2nd	METZ '22
<i>Deromyia winthemi</i>	12 spg.	5 + XY	5 + X 5 + Y	—	—	METZ '16 a
<i>Drosophila affinis</i>	10 oog. 10 spg.	—	—	—	Unequal XY in male	METZ '16 a, '16 b
<i>Drosophila amoena</i>	8 spg. 8 oog.	—	—	—	Unequal XY in male	METZ '14, '16 a, '16 b
<i>Drosophila caribea</i>	8 spg. 8 oog.	—	—	—	Unequal XY in male	METZ '16 b
<i>Drosophila melanogaster</i> ( <i>ampelophila</i> )	8 spg. 8 oog.	3 + XY 4 ♀	— 4 ♀	—	—	STEVENS '08 METZ '14, '16 a, '16 b, '26 b HUETTNER '24

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyle	2nd cyle	tid		
<i>Drosophila</i> <i>obscura</i>	10 spg. 10 oog.	4 + XY 4 + Y	4 + X	—	Unequal XY in male	METZ '16a, '16b, '26b
<i>Drosophila</i> <i>ornatipennis</i>	10 spg. 10 oog.	—	—	—	Unequal XY in male	METZ '16a, '16b
<i>Drosophila</i> <i>repleta</i>	12 spg. 12 oog.	—	—	—	Unequal XY in male	METZ '16a, '16b
<i>Eristalis tenax</i>	12 spg. 12 ♂ soma 12 oog.	5 + XY	5 + X 5 + Y	—	X and Y divide equationally in 2nd	STEVENS '08 METZ '16a
<i>Leptogaster</i> <i>badius</i>	10 spg.	—	5	—	Unequal XY in male	METZ '16a
<i>Lucilia caesar</i>	—	5 + XY	5 + X 5 + Y	—	—	STEVENS '08
<i>Musca domestica</i>	12 spg.	5 + XY	5 + X 5 + Y	—	2 pairs of sex chromosomes seen in one ex- ceptional cell by KEUNECKE. Sex chromosomes divide equatio- nally in 2nd	STEVENS '08 KEUNECKE '24
<i>Phorbia brassica</i>	—	5 + XY	—	—	XY to pole in 1st	STEVENS '08
<i>Phromia regina</i>	12 spg.	5 + XY	5 + X 5 + Y	—	X and Y not paired in 1st?	METZ '16a
<i>Ptetis trivittatus</i>	16 spg.	—	—	—	Unequal XY in male	METZ '16a
<i>Sarcophaga</i> <i>carnaria</i>	12 spg.	5 + XY	5 + X 5 + Y	—	—	KEUNECKE '24
<i>Sarcophaga</i> <i>sarriceniae</i>	12 spg. 12 oog.	5 + XY	5 + X 5 + Y	—	2nd division equational for sex chromosomes	STEVENS '08
<i>Sarcophaga</i> <i>tuberosa (sar- raceniae)</i>	12 spg. 12 oog.	5 + XY	5 + X 5 + Y	—	—	METZ '16a
<i>Scaptomyza</i> <i>adusta</i>	10 spg.	—	—	—	Unequal XY in male	METZ '16b
<i>Scaptomyza</i> <i>graminum</i>	8 spg. 8 oog.	—	4	—	Unequal XY in male	METZ '16a, '16b
<i>Scatophaga</i> <i>pallida</i>	12 spg. 12 oog.	5 + XY	5 + X 5 + Y	—	—	STEVENS '08
<i>Scatophaga</i> <i>stercoraria</i>	12 spg.	5 + XY	—	—	—	KEUNECKE '24

Species	Diploid Chromo-somes Number	Meiotic Chromosomes (male, unless otherwise stated)			Re-marks	Reference
		1st cyte	2nd cyte	tid		
<i>Sciara pauciseta</i> <sup>1</sup>	10 spg. 10 ♂ soma 8 oog.	4 + 2 sl. 4 (degen)	4 + 2 sl. 4 (degen)	3 + 2 sl. + sm. 3 + 2 sl. (degen)	—	METZ '25, '26 a METZ and MOSES '26 METZ, MOSES and HOPPE '26
<i>Sciara prolific</i>	10 spg. 10 ♂ soma 8 oog.	4 + 2 sl. 4 (degen)	4 + 2 sl. 4 (degen)	3 + 2 sl. + sm. 3 + 2 sl. (degen)	—	METZ '25, '26 a, '26 b METZ and MOSES '26 METZ, MOSES and HOPPE '26
<i>Sciara similans</i>	10 spg. 10 ♂ soma 8 oog.	4 + 2 sl. 4 (degen)	4 + 2 sl. 4 (degen)	3 + 2 sl. + sm. 3 + 3 sl. (degen)	—	METZ '25, '26 a, '26 b METZ and MOSES '26 METZ, MOSES and HOPPE '26
<i>Tephritis arnicae</i>	11 spg.	5 + X	5 + X	5 5 + X	—	KEUNECKE '24
<i>Tetanocera sparsa</i>	12 spg. 12 oog.	5 + XY	5 + X 5 + Y	—	—	STEVENS '08
<i>Volucella obesa</i>	12 spg.	5 + XY	—	—	—	METZ '16 a

chromosomes sometimes appear to be joined end to end, in the preparatory phases. Both pass to the same pole while the remaining chromosomes are so distributed that each pole receives one member of each pair. The cell which does not receive the two large chromosomes always degenerates.

In the second division one of the smaller chromosomes passes undivided to one pole, whereas all the others including the large chromosomes, previously undivided, now undergo a normal division. This time the cell which receives one chromosome less than its sister cell is subject to degeneration and the surviving cell then forms a sperm. It is of little use to endeavor to interpret these findings as they stand. It seems absolutely necessary to employ breeding experiments to clear up several of the minor features of the spermatogenesis, and above all to analyze the oogenesis before any conclusion will be justified<sup>2</sup>.

#### HETEROPTERA (HEMIPTERA)

As in case of the Orthoptera, the large number of accounts that take up sex chromosomes in this order makes it advisable to consider the different families separately.

<sup>1</sup> sl. = large chromosome found only in male.

sm. = small chromosome passing undivided to one pole in 2nd spermatocyte division.

<sup>2</sup> A more detailed account has appeared more recently (METZ, MOSES & HOPPE, '27). In addition, evidence has been adduced from breeding experiments (METZ & MOSES, '26) that the female is responsible for the sex of the offspring and that, as the cytological findings indicate, the male produces only one type of sperm.

*Belostomidae*: Investigation of the spermatogenesis seems to demonstrate a simple XY pair in *Belostoma* (MONTGOMERY '01b, '06, CHICKERING '16).

*Capsidae*: MONTGOMERY's accounts of 1901 and 1906 indicate that in *Poecilocapsus* an XY is present in the males. MONTGOMERY's account of two other forms investigated by him does not allow any definite conclusions however.

*Coreidae*: This is one of the families that furnished material for the investigations and discussions which finally culminated in the acceptance of the sex chromosome theory, at least in its general aspects. In great part the disagreements among earlier workers investigating various species belonging to the present family were due to the surprising multiplicity of behavior and appearance which characterizes the sex chromosomes in different species, and also to variations and special peculiarities in certain of the autosomes. When to this are added the almost unavoidable errors that are incurred in every new field, the temporary confusion must seem natural. Mention need be made only of such cases as that of *Anasa tristis* in which for a long time no agreement could be reached on the comparatively simple question of the number of chromosomes in the spermatogonia as well as the more intricate points involved in the interpretation of the chromosome nucleolus in the preparatory phases and the actual distribution of the heterochromosomes with their bearing on sex determination. Again, in *Syromastes* wrong conclusions were reached on the subject of the relation between the m chromosomes and sex chromosomes, as well as on the broader aspects of sex determination, and it was not until WILSON ('09a & c) had pointed out where earlier interpretations had erred that the subject was cleared up.

The behavior and appearance of the sex chromosomes before and during meiosis is highly variable in different species. The X may be larger than any autosome (as in *Protenor*), or it may have the general dimensions of some of the smaller autosomes and be hard to distinguish from them on the score of size (as in *Alydus*). In the preparatory phases of the spermatogonia, the sex chromosomes are not distinguishable because of heteropycnosis, but in the corresponding stages of meiosis their precocious condensation is very marked. During the latter period sex chromosomes may be intimately associated with plasmosomes (*Alydus*, fig. 6B) and again they may be entirely independent of them (*Metapodius*, fig. 8). In cases where the male has an XY pair, these two sex chromosomes may be separated all through the various phases up to the metaphase of the second division, when they may come together for a short interval before passing to opposite poles. On the other hand, the components of a compound X may remain united through both maturation divisions (*Syromastes*). Finally, differences between species may be observed in the behavior of sex chromosomes in the actual divisions, most cases being characterized by a lagging on the spindle (*Leptocoris*, *Syromastes*) while in others they may precede the autosomes to the poles (*Oncopeltus*).

Two sources of confusion in studying the sex chromosomes in the present family lie in the supernumerary and m chromosomes. The latter were confused by PAULMIER, GROSS, and at first also by MONTGOMERY with sex chromosomes. WILSON ('05b) showed however that they can

be differentiated from sex chromosomes in several ways. The smallest chromosomes in nearly all cases, they are not precociously condensed in the growth stages of the maturation period except occasionally in *Alydus pilosulus* and *Archimerus calcarator*. Except in some cases like the aberrant occurrences of *Metapodius*, they are always two in number. Separated in the growth stages and prophases, they come together for an instant in the first spermatocyte plate only to separate again immediately and pass to opposite poles. In the second division they divide equationally. In other words, their behavior is just opposite to that of the sex chromosomes in this family in that for the latter, reduction occurs in the second while for the m chromosomes it occurs in the first division. It is also of some importance to note that the extra m chromosomes in some forms of *Metapodius* form their brief union with the two m chromosomes normally present but never unite with the sex chromosomes (WILSON, '05b, '07b, '07c, '09b, '10a).

The supernumeraries which in case of *Metapodius* (fig. 8) may increase the diploid number of chromosomes from 22 to 28, are believed by WILSON ('07c, '09b, '10a) to have originated through nondisjunction of the Y chromosome, and he explains the fact that they are frequently smaller than the normal Y on the basis that they are degenerating and on the way to disappearance. With sex chromosomes these supernumeraries share the feature of precocious condensation, and their relationship is more directly shown by the fact that they often unite with the normal XY pair to form a single chromosome nucleolus during the early preparatory stages of the spermatocytes. In the first division they once more become independent and divide equationally, just like the sex chromosomes.

In a general review of sex chromosomes as they occur in the family, the following classification might be made:

a) Cases in which males represent the XO and the females the XX condition. The diploid number of the female always exceeds that of the male by one chromosome. In all *Coreidae* except one, the unpaired X of the male passes undivided to one pole in the second and divides equationally in the first spermatocyte division. The exception is furnished by *Archimerus calcarator* where the two maturation divisions take place in the reverse order.

b) Cases in which the male has an unpaired compound X and the female a pair of such X chromosomes (male =  $X^I + X^{II}$ ; female =  $2 X^I + 2 X^{II}$ ). Just as in the simple X condition, the reduction division for the sex chromosomes in the male is the second, both components behaving like a unit and passing together to one pole.

c) Cases in which the male shows the XY and the female the XX condition. Again as in the previous cases, the first spermatocyte division is equational for the XY, and the second is reductional—X and Y passing to opposite poles.

*Galgalidae*: The only species investigated is *Gelastocoris (Galgalus) oculatus*. PAYNE ('09a, '12) found the sex chromosomes of the male to be comprised of a compound X of 4 components and a single Y. The 4 elements of the X act as a unit, passing together to one pole in the second division while the Y passes to the opposite pole. The components of this compound X behave as independent units during

the somatic divisions, the diploid number found in the male's somatic cells is 35 chromosomes. As might be expected from the assumption that the female has 2 compound X chromosomes, the diploid number in that sex is 38.

*Hydrometridae*: MONTGOMERY's account of the spermatogenesis in two species makes it likely that the males there have a simple XO in condition, with segregation of the X occurring in the second spermatocyte division. Very peculiar conditions were however described by WILKE ('07, '12, '13) in two species *Hydrometra*. According to this investigator the spermatogenesis presents such puzzling aspects as a spermatogonial number equal to a spermatocyte number of chromosomes, a pair of heterochromosomes uniting in the spermatogonia, and a division of each of these 2 heterochromosomes in both spermatocyte divisions. WILKE's account is so confusing that only a reinvestigation of the species in question would warrant any conclusions.

*Lygaeidae*: MONTGOMERY's and WILSON's work on various species shows the XY condition prevailing in the males (fig. 2). Only in *Oedancala* is there an indication of an unpaired X, although MONTGOMERY's description is too inconclusive to make this certain. An illuminating case is that of *Oncopeltus*, where WILSON ('09a, '12) demonstrated that the X and Y behave just as in the other species but are exactly alike in size. It is thus evident that inequality in size is an insufficient criterion for the recognition of an XY pair.

*Nabidae*: MONTGOMERY's account of two species in this family is incomplete. However it seems that the male of *Nabis* shows an XY.

*Naucoridae*: In the spermatogenesis of *Naucoris maculatus*, POISSON ('21) has described several peculiar features. Thus the number of chromosomal bodies in the first spermatocyte is 17, while the second spermatocyte shows only 16, a fact possibly due to a fusion of the two m chromosomes in the latter cell. Another chromosome is subject to heteropycnosis and lags on the spindle. It divides in both spermatocyte divisions. The evidence either for or against regarding this chromosome as a sex chromosome is incomplete, especially as POISSON does not give any figures.

*Nepidae*: CHICKERING ('18) reported the XY condition for the male of a species of *Ranatra*. His evidence is insufficient. For another member of the family, *Nepa cinerea*, two workers have published conflicting accounts. SPAUL ('22) reported that the male has a diploid number of 35 and that the single X chromosome has no partner, whereas STEOPOE ('25) found 33 chromosomes in spermatogonial cells and concluded that the sex chromosomes of the male are represented by an X of 4 components and a single Y. The status of the family is therefore far from definite.

*Notonectidae*: In various species of *Notonecta*, males show an XY pair and females 2 X. Special interest attaches to the fact that in some of the species the X of the male betrays the tendency to break up into smaller components (fig. 28). This is especially marked in *N. indica*, and BROWNE ('10, '13, '16) suggested that we have here a case in which the intermediate condition between the single X and the X which is found only in the form of separated components is represented.

*Pentatomidae*: Sex chromosome conditions are remarkably homogeneous in this family. All males have the XY and all females the 2 X condition. In the growth period of the spermatocytes, the X and Y frequently come together to form a single chromosome nucleolus but with the possible exception of *Pentatoma senilis* (where they retain

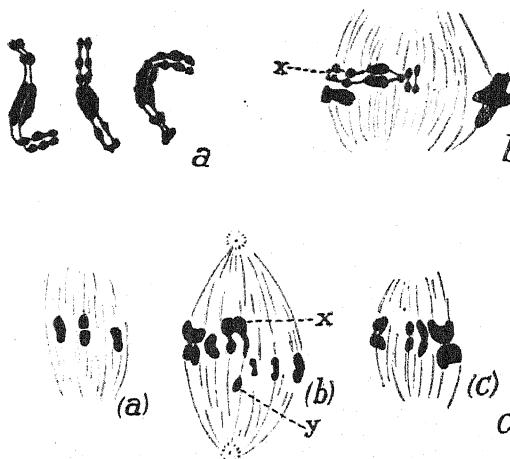


Fig. 28. *Notonecta indica* (BROWNE, '16)—a Three figures of the X in early prophase of first spermatocyte. b First spermatocyte division in which X divides equationally. c Second spermatocyte division in which X and Y separate after joining in the metaphase. Figure shown in 3 sections.

some kind of a connection through the first division (fig. 5), this union is broken before the first metaphase plate is formed. The first or equational division then occurs in each sex chromosome entirely independently of the other. As in so many other Hemiptera, the X and Y come together for a moment prior to the second division and then pass to opposite poles.

In most cases the two sex chromosomes of the male show a notable size dimorphism, the Y always constituting the smaller member of the pair. In *Nezara hilaris* however, they are practically equal in size (fig. 29). *Thyanta calceata* provides the only example of a compound X, there being 2 components. In some specimen of *Banasa calva* (those from Long Island) a supernumerary is found. It does not behave like the sex chromosomes of that species but goes undivided to one pole in the first spermatocyte division. The sex chromosomes themselves are however distributed in the usual manner and are apparently quite independent of the supernumerary (WILSON, '07c).

*Phymatidae*: MONTGOMERY's insufficient evidence ('01) suggests that males of *Phymata* have an unpaired X.

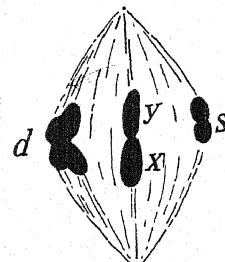


Fig. 29. *Nezara hilaris* (WILSON, '11)—Second spermatocyte division in which X and Y appear almost equal in size.

*Pyrrhocoridae*: On *Pyrrhocoris apterus* HENKING ('91) made the famous observations which entitle him to the credit of having been the first to describe sex chromosomes. Strangely enough, the correct interpretation of the sex chromosome conditions in this species was not made until many years later (WILSON, '09 a, '09 c). The number of chromosomes in the spermatogonia is 23 and in the oogonia 24. The course of spermatocyte divisions shows definitely that the male has an unpaired X and the number of chromosomes in the oogonia fully confirms the assumption that the female has a pair of X chromosomes. That this simple condition was not recognized until 1909 was due in part to the fact that HENKING himself believed the spermatogonial number to be 24, but also to the fact that GROSS ('06, '12), who could not convince himself of the validity of the sex chromosome hypothesis, insisted that the spermatogonial number given by HENKING is the correct one. An XO for the male and 2 X for the female was also established for two species of *Largus* by WILSON (07 a, '09 a, '09 c).

*Reduviidae*: Here are presented some of the most interesting conditions of sex chromosomes among insects. With the exception of the somewhat cursory report on a few of the forms given by MONTGOMERY ('01 b, '06), the elucidation of these conditions is the work of PAYNE ('09 a, '10, '12). The simplest condition is represented in *Apiomeris*, *Diplocodus*, and *Reduvius*, where the males show an unequal XY pair which in meiosis behaves in the manner typical of the great majority of Hemiptera, i. e. both X and Y divide equationally in the first and pass to opposite poles in the second division. In case of *Conorhinus*, *Fitchia*, and *Rocconata* conditions are just like those shown in the three species already mentioned, except for the fact that in each case there is a compound X of 2 components; in *Prionidus* (fig. 7), *Pselliodes* and four species of *Sinea* the X has 3 components; in *Pnirontis* the X has 4 components; and in the extreme cases of *Acholla* (fig. 30) and *Sinea rileyi* the X has 5 components. Regardless of the number of components of the X, only one Y chromosome is present in all these forms. Again, although usually no visible connection exists between components of the X, they nevertheless behave like a single X, dividing equationally in the first spermatocyte and passing together to the pole opposite to that of the Y in the second spermatocyte division. The evidence seems to show that in the metaphase plate of the first division the sex chromosomes generally show no special arrangement, but that in the second metaphase plate their position is more or less constant for any one species—the components of the X forming a flat group with the Y directly above or below them. The amount of chromation in even the extreme cases of the compound X is not exceptionally large, and in a few cases, notably *Acholla* (fig. 30), it is markedly smaller than that of the single Y. All these aspects led PAYNE to suggest that (09) the compound X as seen in these species represents nothing more than an ordinary and single X that has undergone fragmentation, a fragmentation not haphazard but no doubt based on the basic structure of the original X.

In some of the cases the actual distribution of the sex chromosomes to the spermatids has not been observed. However, the facts are quite clear as a study of the diploid numbers of both sexes demon-

## HETEROPTERA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	References
		1st cyte	2nd cyte	tid		
1. <i>Belostomatidae</i>						
<i>Belostoma (Zaitza) fluminea</i>	24 spg.	13	11 + XY 11 + Y	11 + X 11 + Y	—	CHICKERING '16
<i>Belostoma</i> sp.	24 spg.	13	11 + XY	11 + X 11 + Y	—	MONTGOMERY '01 b, '06
2. <i>Capsidae</i>						
<i>Calocoris rapidus</i>	30 spg.	16	15 16	—	1 of the 2 sex chromosomes passes to pole in each division	MONTGOMERY '01, '06
<i>Lygus pratensis</i>	35? spg.	19	—	—	Small chromosome of 1st not found in 2nd. X and Y to opposite poles in 2nd?	MONTGOMERY '01, '06
<i>Poecilocapsis goniphorus</i>	—	18 (16 + X + Y)	16 + XY	16 + X 16 + Y	—	MONTGOMERY '01, '06
3. <i>Coreidae</i>						
<i>Alydus eurinus</i>	13 spg.	6 + X	6 + X	6 6 + X	—	MONTGOMERY '01b, '04, '06
<i>Alydus pilosulus</i>	13 spg. 14 oog. 14 ♀ soma	6 + X	6 + X	6 6 + X	—	MONTGOMERY '01b, '06 WILSON '05b, '06
<i>Anasa armigera</i>	21 spg. 22 oog.	10 + X	—	—	—	MONTGOMERY '01 b, '06 WILSON '05b, '09 a
<i>Anasa tristis</i>	21 spg. 22 oog. 22 ♀ soma	10 + X 11 ♀	10 + X 11 ♀	10 10 + X	—	PAULMIER '98, '99 MONTGOMERY '01b, '04, '06 WILSON '05a, '05 b, '06, '07 a, '11 FOOT & STROBELL '07 a, '07 b LEFEVRE & MCGILL '08 MC CLUNG & PINNEY '10 MORRILL '09, '10 HOY '14, '16 8*

Species	Diploid Chromo-some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	References
		1st cyte	2nd cyte	tid		
<i>Anasa</i> sp.	21 spg. 22 oog.	10 + X	10 + X	—	—	MONTGOMERY '01b, '04, '06
<i>Archimerus alternatus</i> ( <i>calcarator</i> ?)	15 spg. 16 oog. 15 & 16 embryos	8 8 ♀	8 ♀	8 ♀	—	MORRILL '09, '10
<i>Archimerus calcarator</i>	15 spg.	7 + X	7 + X 7	—	—	WILSON '05a, '05b, '09a
<i>Catorintha</i> sp.?	25 spg.	—	—	—	Probably male XO	WILSON '07a
<i>Chariesterus antennator?</i>	21 spg.	—	—	—	X to pole in 2nd	WILSON '05a, '05b
<i>Chariesterus antennator</i>	25 spg. 26 oog.	13 + X	13 + X	13 13 + X	—	MONTGOMERY '01b, '06 WILSON '09a
<i>Chelinidea vittigera</i>	21 spg. 22 oog. 21 & 22 clv.	—	—	—	Male probably XO	WILSON '07a MORRILL '09, '10
<i>Corizus alternatus</i>	13 spg.	6 + X	6 + X	6 6 + X	—	MONTGOMERY '01a, '01b, '04, '06
<i>Corizus lateralis</i>	—	6 + X	6 + X	6 6 + X	—	MONTGOMERY '01b, '06
<i>Corynocoris distinctus</i>	25 spg. 26 oog.	—	—	—	Male probably XO	WILSON '09a
<i>Euthoëtha galeator</i>	21 spg. 22 oog.	—	—	—	Male probably XO	WILSON '07a, '09a
<i>Harmostes reflexulus</i>	13 spg. 14 oog.	6 + X	6 + X	6 6 + X	—	MONTGOMERY '01a, '01b, '04, '06 WILSON '06
<i>Leptocoris haematooma</i>	13 spg.	6 + X	6 + X	6 6 + X	—	MONTGOMERY '01a, '01b, '04, '06 WILSON '06
<i>Leptocoris trivittatus</i>	13 spg. 14 oog.	6 + X	6 + X	6 6 + X	—	WILSON '07a, '09a PORTER '17 YOCOM '23
<i>Leptoglossus phyllopus</i>	21 spg.	10 + X	—	—	X to pole in 2nd	WILSON '07a, '09a, '11
<i>Margus inconspicuus</i>	23 spg. 24 oog.	—	—	—	♂ probably XO	WILSON '07, '09a

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	References
		1st cyte	2nd cyte	tid		
<i>Metapodius femoratus</i>	22 spg. 22 oog.	10 + X + Y	10 + X + Y	10 + X 10 + Y	Numerical variation due to extra m, supernumeraries (= y?) and absence of X	WILSON '07b, '09b, '10a
<i>Metapodius granulosus</i>	22 spg. 22 oog.	10 + X + Y	10 + X + Y	10 + X 10 + Y	Numerical variation due to extra m, supernumeraries (= y?) and absence of X	WILSON '07b, '09b
<i>Metapodius terminalis</i>	22 spg. 22 oog.	10 + X + Y	10 + X + Y	10 + X 10 + Y	Numerical variation due to extra m, supernumeraries (= y?) and absence of X. Y absent in 1 male	MONTGOMERY '01b, '06 WILSON '07a, '07b, '07c, '09b
<i>Narnia</i> sp.?	21 spg.	—	—	—	Male probably XO	WILSON '07a
<i>Pachylis gigas</i>	15 spg. 16 oog.	7 + X	—	—	Male probably XO	WILSON '07a, '09a, 11
<i>Protenor belfragei</i>	13 spg. 14 oog. 13 & 14 clv. 14 ♀ soma	6 + X 7	6 + X	6 6 + X 7	—	MONTGOMERY '01b, '04, '06 WILSON '05b, '06, '11, '12 MORRILL '10, '09
<i>Syromastes marginatus</i>	22 spg. 24 oog.	10 + X <sup>I</sup> X <sup>II</sup>	10 + X <sup>I</sup> X <sup>II</sup>	10 + X <sup>I</sup> + X <sup>II</sup> 10	—	WILSON '09a, '09c GROSS '04a, '04b, '12
4. <i>Galbulidae</i>					—	
<i>Galbulus (Gelastocoris) oculatus</i>	35 spg. 38 oog.	20	15 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + Y	15 + Y 15 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup>	—	PAYNE '09a, '12
5. <i>Hydrometridae</i>					—	
<i>Hydrometra lacustris</i>	11 spg.	12	12	—	1 large spermatogonial chromosome forms 2 in cytes	WILKE '07, '13
<i>Hydrometra paludum</i>	10—15 spg.?	12	12	—	Thinks sex chromosome divides in both divisions	WILKE '12, '13

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Hydrotrechus</i> sp.?	21 spg. (probably)	11	11	10 10 + X	—	MONTGOMERY '01b, '06
<i>Limnotrochus</i> <i>marginatus</i>	—	10 + X	10 + X	—	X to pole in 2nd	MONTGOMERY '01b, '06
6. <i>Lygae-</i> <i>idae</i>	—	—	—	—	—	—
<i>Cymus</i> <i>angustatus</i>	—	—	18 + XY	—	—	MONTGOMERY '01b, '06
<i>Cymus</i> <i>luridus</i>	—	15	—	—	—	MONTGOMERY '01a
<i>Ichnodemus</i> <i>falciculus</i>	15 (16?) spg.	7 + X + Y	7 + X + Y	—	—	MONTGOMERY '01b, '06
<i>Lygaeus</i> <i>birrucis</i>	14 spg. 14 oog.	6 + X + Y	6 + X + Y	6 + X 6 + Y	—	WILSON '09a, '12
<i>Lygaeus</i> <i>turcicus</i>	14 spg. 14 oog.	6 + X + Y	6 + X + Y	6 + X 6 + Y	—	WILSON '05a, '05b, '06
<i>Oedancala</i> <i>dorsalis</i>	13 spg.	7	7	6 7	♂ = XO?	MONTGOMERY '01b, '04, '06
<i>Oncopeltus</i> <i>fasciatus</i>	16 spg. 16 oog.	7 + X + Y	7 + X + Y	7 + X 7 + Y	X and Y equal in size in some cells	MONTGOMERY '01b, '06 WILSON '09a, '12
<i>Peliopelta</i> <i>abbreviata</i>	14 spg.	6 + X + Y	6 + X + Y	—	X and Y to poles in 2nd probably	MONTGOMERY '01b, '06
7. <i>Nabidae</i>	—	10	—	—	XO or XY, not certain	MONTGOMERY '01b
<i>Coriscus</i> <i>ferus</i>	—	—	—	—	—	—
<i>Nabis</i> <i>annulatus</i>	—	8 + X + Y	8 + X + Y	8 + X 8 + Y	—	MONTGOMERY '01a, '06
8. <i>Nepidae</i>	—	—	—	—	—	—
<i>Nepa</i> <i>cinerea</i>	—	—	—	—	SPAUL reported XO STEOPOE reported X <sup>I</sup> X <sup>II</sup> X <sup>III</sup> X <sup>IV</sup> Y	SPAUL '22 STEOPOE '25
<i>Banatra</i> sp.?	40 spg.	21	19 + XY	19 + X 19 + Y	—	CHICKERING '18
9. <i>Notonectidae</i>	—	—	—	—	—	—
<i>Notonecta</i> <i>glauca</i>	24 spg. (?) 24 oog.	11 + X + X	11 + XY	11 + X 11 + Y	—	PANTEL & DE SINETEY '06 BROWNE '10, '13, '16
<i>Notonecta</i> <i>indica</i>	26 spg. 26 oog.	12 + X + Y	12 + XY	12 + X 12 + Y	X composed of 5 elements	BROWNE '16
<i>Notonecta</i> <i>insulata</i>	—	12 + X + Y	12 + XY	12 + X 12 + Y	2 autosomes sometimes fuse	BROWNE '10, '13, '16

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Notonecta irrorata</i>	24 spg. 24 oog.	11 + X + Y	11 + XY 11 + Y	11 + X 11 + Y	—	BROWNE '10, '13, '16
<i>Notonecta shooteri</i>	26 spg. 26 oog.	12 + X + Y	12 + XY 12 + Y	12 + X 12 + Y	—	BROWNE '16
<i>Notonecta undulata</i>	26 spg. 26 oog.	12 + X + Y	12 + XY 12 + Y	12 + X 12 + Y	—	BROWNE '10, '13, '16
10. <i>Pentatomidae</i>						
<i>Banasa calva</i>	26 spg. 26 oog.	12 + X + Y	12 + X + Y	12 + X 12 + Y	Supernumerary in some species — goes to pole in 1st	WILSON '05b, '07c
<i>Banasa dimidiata</i>	16 spg.	7 + X + Y	7 + XY 7 + Y	7 + X 7 + Y	—	WILSON '07c
<i>Brochymena</i> sp.?	14 spg.	6 + X + Y	6 + XY 6 + Y	6 + X 6 + Y	—	MONTGOMERY '01b, '06 WILSON '05a, '06
<i>Coenus delius</i>	14 spg. 14 oog.	6 + X + Y	6 + XY 6 + Y	6 + X 6 + Y	—	MONTGOMERY '01b, '06 WILSON '05a, '06
<i>Cormopepla carnifex</i>	16 spg.	7 + X + Y	7 + XY 7 + Y	7 + X 7 + Y	—	MONTGOMERY '01b, '06
<i>Eurygaster alternatus</i>	—	5 + X + Y	5 + XY 5 + Y	5 + X 5 + Y	—	MONTGOMERY '01b, '06
<i>Euschistus crassus</i>	12 spg. 12 oog.	5 + X + Y	5 + XY 5 + Y	5 + X 5 + Y	—	FOOT & STROBELL '12
<i>Euschistus fissilis</i>	14 spg. 14 oog.	6 + X + Y	6 + XY 6 + Y	6 + X 6 + Y	—	WILSON '05a, '05b
<i>Euschistus ictericus</i>	14 spg. 14 oog.	—	—	—	XY in male	WILSON '06
<i>Euschistus servus</i>	14 spg. 14 oog.	6 + X + Y	6 + XY 6 + Y	6 + X 6 + Y	—	FOOT & STROBELL '14 WILSON '06
<i>Euschistus tristigmus</i>	14 spg.	6 + X + Y	6 + XY 6 + Y	6 + X 6 + Y	—	MONTGOMERY '01b, '06 WILSON '06
<i>Euschistus variolarius?</i>	14 spg.	6 + X + Y	6 + XY 6 + Y	6 + X 6 + Y	—	MONTGOMERY '01b, '06
<i>Euschistus variolarius</i>	14 spg. 14 oog.	6 + X + Y	6 + XY 6 + Y	6 + X 6 + Y	—	FOOT & STROBELL '14 WILSON '06

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Mineus bioculatus</i>	14 spg. 14 oog.	—	—	—	XY in male	WILSON '06
<i>Mormidea lugeus</i>	14 spg.	6 + X + Y	6 + XY	—	XY to poles in 2nd	MONTGOMERY '01b, '06
<i>Nezara hilaris</i>	14 spg. 14 oog.	6 + X + Y	6 + XY	6 + X 6 + Y	X and Y almost equal	MONTGOMERY '01b, '06 WILSON '06, '11
<i>Nezara viridula</i>	14 spg. 14 oog.	6 + X + Y	6 + XY	6 + X 6 + Y	—	WILSON '11
<i>Oebalus pugnax</i>	10 ♂ soma 10 ♀ soma	—	—	—	XY in male	WILSON '09a
<i>Pentatomidae (Rhytidomia) senilis</i>	6 spg.	2 + X + Y	2 + X + Y	2 + X 2 + Y	X and Y sometimes united in 1st	WILSON '13
<i>Peribalus limbolaris</i>	14 spg.	6 + X + Y	6 + XY	6 + X 6 + Y	—	MONTGOMERY '01b, '06
<i>Perillus confluens</i>	14 spg.	6 + X + Y	6 + XY	6 + X 6 + Y	—	MONTGOMERY '01b, '06
<i>Podisus bracteatus</i>	14 spg.	—	—	—	—	WILSON '09c
<i>Podisus crocatus</i>	14 spg.	—	—	—	—	WILSON '09c
<i>Podisus maculiventris</i>	16 spg.	7 + X + Y	7 + XY	7 + X 7 + Y	—	MONTGOMERY '01b, '06 WILSON '05a, '06
<i>Podisus modestus</i>	16 spg.	—	—	—	—	WILSON '09c
<i>Podisus placidus</i>	16 spg.	—	—	—	—	WILSON '09c
<i>Podisus spinosus</i>	16 spg.	7 + X + Y	7 + XY	7 + X 7 + Y	—	WILSON '05a, '06
<i>Stiretrus anchorago</i>	14 ♂ soma 14 ♀ soma	—	—	—	XY in male	WILSON '09a
<i>Thyanta calceata</i>	27 spg. 28 oog.	12 + X <sup>I</sup> + X <sup>II</sup> + Y	—	—	X <sup>I</sup> + X <sup>II</sup> + Y in male	WILSON '09c, '11
<i>Thyanta custator</i>	16 spg. 16 oog.	—	—	—	XY to poles in 2nd	WILSON '11
<i>Trichopepla semivittata</i>	15 or 16 spg. (at least)	6 + X + Y	6 + XY	6 + X 6 + Y	Nature of the 2 small elements in spg. and 1st cytes not clear	MONTGOMERY '01b, '06 WILSON '05a

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
11. <i>Phymatidae</i>						
<i>Phymata wolffii?</i>	29 spg. (probably)	15	—	—	Male possibly XO	MONTGOMERY '01b, '06
12. <i>Pyrrhocoridae</i>						
<i>Largus cinctus</i>	11 spg. 12 oog.	—	—	—	Male is XO	WILSON '07a, '09a, '09c
<i>Largus succinctus</i>	13 spg. 14 oog.	—	—	—	Male is XO	WILSON '07a, '09a, '09c
<i>Pyrrhocoris apterus</i>	23 spg. 24 oog.	11 + X 12 ♀	11 + X 12 ♀	11 11 + X 12 ♀	HENKING & GROSS believed spg. = 24	HENKING '90, '91, '92 GROSS '06, '12 WILSON '09a, 09c
13. <i>Reduviidae</i>						
<i>Acholla ampliata</i>	32 spg.?	16	16	—	PAYNE '09a thinks MONTGOMERY called this <i>A. multispinosa</i> ? Apparently has 4 sex chromosomes	MONTGOMERY '01b, '06
<i>Acholla multispinosa</i>	30 oog. 26 spg.	10 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> + Y (= 16)	10 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> + Y (= 16)	10 + Y (= 11)	2 X elements joined to Y in prophases up to 2nd division (MONTGOMERY calls this <i>Sinea diadema</i> , PAYNE '09)	PAYNE '09a, '10
<i>Apiomeris crassipes</i>	24 spg.	13	13	—	XY to pole in 2nd	PAYNE '12
<i>Conorhinus sanguisugus</i>	23 spg.	10 + X <sup>I</sup> + X <sup>II</sup> + Y	10 + X <sup>I</sup> + X <sup>II</sup> + Y	10 + X <sup>I</sup> + X <sup>II</sup> 10 + Y	—	PAYNE '09a, '12
<i>Diplocodus exsanguis</i>	26 spg. 26 oog.	12 + X + Y	12 + X + Y	—	XY to pole in 2nd	PAYNE '09a
<i>Fitchia spinosula</i>	27 spg. 28 oog.	12 + X <sup>I</sup> + X <sup>II</sup> + Y	12 + X <sup>I</sup> + X <sup>II</sup> + Y	—	X <sup>I</sup> X <sup>II</sup> and Y probably to opposite poles in 2nd	PAYNE '09a
<i>Pnirontis modesta</i>	25 spg.	15	10 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + Y	—	Probably X <sup>I</sup> X <sup>II</sup> X <sup>III</sup> X <sup>IV</sup> and Y to opposite poles in 2nd	PAYNE '12

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Prionidus cristatus</i>	26 spg. 28 oog.	11 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + Y	11 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + Y	—	X <sup>I</sup> X <sup>II</sup> X <sup>III</sup> and Y to opposite poles in 2nd	MONTGOMERY '01 b, '06 PAYNE '09a
<i>Psellioides cinctus</i>	28 spg. 30 oog.	16	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + Y	—	Probably X <sup>I</sup> X <sup>II</sup> X <sup>III</sup> and Y to opposite poles in 2nd	PAYNE '12 GOLDSMITH '16
<i>Reduvius personatus</i>	—	12	11	—	♂ = XY probably	PAYNE '12
<i>Roceonata annulicornis</i>	27 spg.	12 + X <sup>I</sup> + X <sup>II</sup> + Y	12 + X <sup>I</sup> + X <sup>II</sup> + Y	12 + X <sup>I</sup> + X <sup>II</sup> 12 + Y	—	PAYNE '09a
<i>Sinea diadema</i>	28 spg. 30 oog.	16	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + Y	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> 12 + Y	—	MONTGOMERY '01 b, '06 PAYNE '09a
<i>Sinea complexa</i>	28 spg. 30 oog.	16	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + Y	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> 12 + Y	—	PAYNE '12
<i>Sinea confusa</i>	28 spg. 30 oog.	16	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + Y	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> 12 + Y	—	PAYNE '12
<i>Sinea rileyi</i>	—	18	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + X <sup>IV</sup> + X <sup>V</sup> + Y	—	Probably X <sup>I</sup> X <sup>II</sup> X <sup>III</sup> X <sup>IV</sup> X <sup>V</sup> and Y to oppo- site poles in 2nd	PAYNE '12
<i>Sinea spinipes</i>	28 spg. 30 oog.	16	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> + Y	12 + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup> 12 + Y	—	PAYNE '12
14. <i>Tingitidae</i>	—	7	7	7	X and Y to poles in 1st?	
<i>Tingis clavata</i>	—	7	7	7		MONTGOMERY '01a, '06

strates. As may be expected, the females carrying 2 X as in other Hemiptera, show no trace of a Y, but twice as many X components as the males. Unfortunately no exhaustive study of the complete oogenesis has been reported in any species.

A study of the preparatory phases of the spermatocytes shows that the material of the sex chromosomes may at that time be contained in one large nucleolus, to the construction of which a plasmosome may also

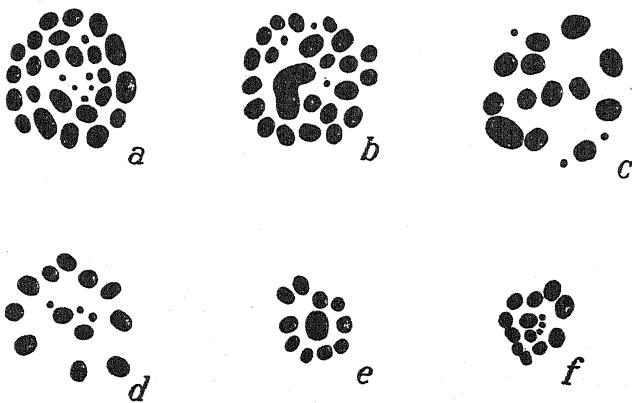


Fig. 30. *Acholla multispinosa* (PAYNE, '10)—*a* Metaphase of oogonial division. 30 chromosomes, including 2 compound X chromosomes of 5 components each. *b* Spermatogonial division. 26 chromosomes, including one compound X of 5 components and a large Y. *c* First spermatocyte metaphase. *d* Second spermatocyte metaphase. *e* & *f* Daughter plates of second spermatocyte division showing 10 autosomes and a large Y, the other 10 autosomes and the 5 components (2 medium and 3 small) of the compound X.

contribute. Shortly before the final condensation of the autosomes, the sex chromosomes emerge from the nucleolus and the plasmosome constituent disappears (Fig. 7).

*Tingitidae*: MONTGOMERY's brief mention of conditions in *Tingis* ('01a, '06) is inconclusive.

#### HOMOPTERA

Sex chromosomes as found in a number of families in this order show such uniformity in structure and behavior that these families may well be considered together. On the other hand in the two families of *Aphididae* and *Coccidae* are encountered features so exceptional that it was thought best to give these two groups special treatment.

*Aphididae*: Analyses of the complicated life cycles of these insects have furnished some excellent demonstrations of the mechanism of the distribution of sex chromosomes and its relation to sex determination. A life cycle of a comparatively simple type is found in *Phylloxera caryaecaulis*. Here there are two kinds of stem mothers. One of these gives rise to winged, migrant females which in turn produce nothing but

males. The other type of stem mother, externally indistinguishable, gives rise to migrants that produce sexual females. Fertilization of sexual females by males finally results in the production of stem mothers again. The case presents a so called closed cycle, the various forms appearing in regular and serial succession. In other species there may be an open cycle and no such serial regularity obtains.

VON BAEHR, MORGAN, and STEVENS have shown that complicated though these cycles are, the chromosomal phenomena conform to what might be expected from our experience with simpler cases. The eggs

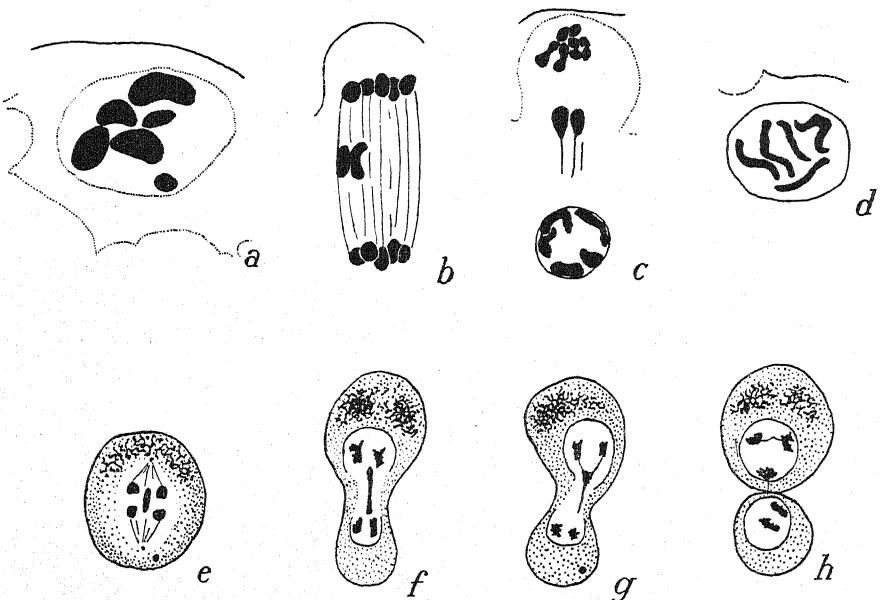
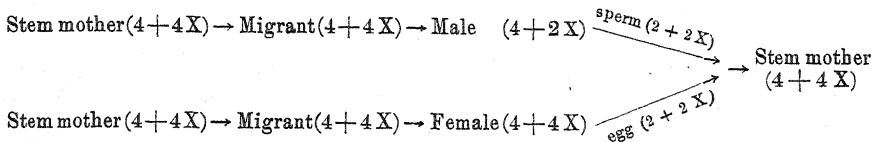


Fig. 31. *Phylloxera caryaecaulis* (MORGAN, '12)—*a* Metaphase of male producing egg. *b* Anaphase of male producing egg showing the lagging split sex chromosome. *c* Telophase of male producing egg with lagging split sex chromosome. *d* Chromosomes in nucleus of male producing egg, with the undivided sex chromosome in the polar body at periphery. *Aphis saliceti* (v. BAEHR, '08)—*e, f, g & h* First spermatocyte division showing unequal distribution of chromosomes and cytoplasmic inclusions.

of stem mothers and migrants developing without fertilization, undergo only one maturation division. This is equational and the chromosomes are not reduced as a consequence—except in the case of male producing eggs. In the latter there is an elimination of one or more chromosomes during the division in question, and there can be little doubt that these are sex chromosomes (fig. 31). The fact that the fertilized sexual eggs always give rise to females, i. e. stem mothers, is in turn due to the peculiar course of meiosis in the males. In the first spermatocyte division certain chromosomes—again sex chromosomes—pass undivided into one of the cells (fig. 31). It is this cell which after a normal equational division gives rise to sperms, while the sister cell degenerates (usually, but not always, without a second division).

The chromosome cycle may be diagrammatically shown as follows:



It must be pointed out that although the correlation between the production of the various types of individuals and the chromosomal phenomena is in general fairly clear, several points remain to be explained. These may be outlined as follows:

a) In cases like *Phylloxera caryaecaulis*, the male producing and the female producing migrants always arise from different stem mothers. Despite the fact that the stem mothers all look alike, there must thus be two types. MORGAN ('09, '12) on the basis of somewhat inconclusive observations suggested that in some migrants one of the small X components exhibits a tendency to attach itself to one of the large X components. Depending then on whether this attached small X or the independent small X are eliminated in the male producing egg, two kinds of males would be produced. The sperms of these in turn after fertilizing the sexual eggs would bring about the production of the two types of stem mothers.

b) The exact way in which certain chromosomes are eliminated from the male producing eggs is not quite clear. STEVENS ('10) suggested that in the aphid of *Oenothera* one of 2 X chromosomes passes bodily into the polar body, thus leaving only a single X in the developing egg. MORGAN's evidence ('08, '09a, '09b, '12, '15) showed that in the male producing egg of *Phylloxera caryaecaulis* 2 components of the X complex (one member of the large and one of the small pair) are thrown out into the polar body. VON BAEHR ('20) however expressed some doubts as to the details of this process—especially as concerns the aphids—and pointed out that in such a case as *Aphis saliceti* the elimination of one sex chromosome may occur in one of two ways: (1.) one of the 2 X chromosomes passes out into the polar body after they have conjugated, or (2.) one X passes undivided into the polar body while the other divides equationally like the autosomes. VON BAEHR's evidence resting on a single egg indicated that already before maturation only a single sex chromosome is found in the egg, but this furnishes an admittedly insufficient basis even for hypothetical considerations. Certain it is that some elimination occurs.

c) Mention should be made of the fact that neither in the oogenesis nor the spermatogenesis has heteropycnosis been observed. VON BAEHR ('09) and MORGAN ('15) both figure a nucleolus in the growth stages of the spermatocytes, but this disappears before the division occurs and is no doubt identical with a true plasmosome. MORGAN believed that the larger of the second spermatocytes of *Phyllaspis coweni* shows that certain of the chromosomes condense slightly faster than the others, but VON BAEHR apparently did not make any such observation in other species. In general then, except in those cases where the sex chromosomes are distinguished by size or form, there is no way of recognizing

them in phases other than the actual divisions, and then only if they lag or precede on the spindle.

d) It has been claimed that in the first spermatocyte division the distribution of the sex chromosomes is predetermined, since they are always found in the larger of the two resulting cells—the same which also contains the main mass of mitochondria. However, it is exceedingly difficult to decide whether the sex chromosomes pass into the larger cell, or whether most of the cell constituents follow the sex chromosomes. On the whole, figures of the process seem to favor the former interpretation, so that here the constitution of cells would regulate distribution of chromosomes and the latter is not left to chance.

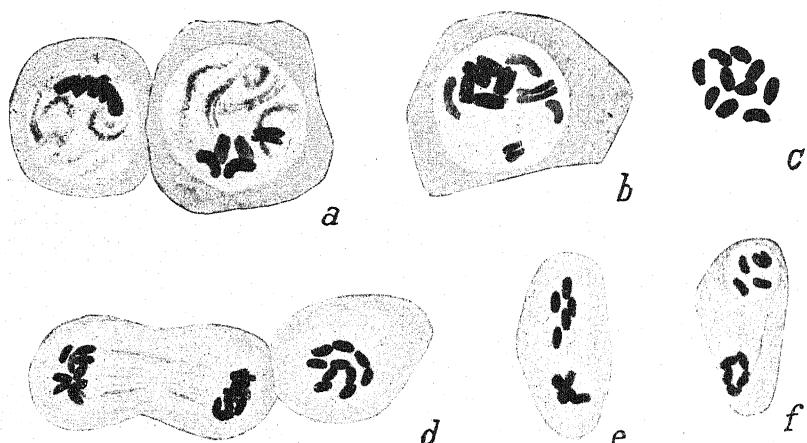


Fig. 32. *Pseudococcus maritimus* (SCHRADER, '23)—a Heteropycnosis involving 5 of the 10 chromosomes in the first spermatocyte. b Later prophase of the first spermatocyte. c Metaphase of first spermatocyte. d Anaphase of first spermatocyte division. e Anaphase of second spermatocyte division. f Telophase of second division.

But regardless of whether these difficulties are solved, it appears clear that in all cases investigated the males are heterogametic. Through a special mechanism females may in some instances produce two kinds of eggs, but these always develop parthenogenetically and are not gametes in the usual sense. The heterogamety of the male expresses itself in the fact that its sex chromosomes have the formula XO. Complications may however arise from the fact that the X chromosome is often compound. The females, no matter what form they may take, are always represented by the XX condition. (Thus in *Phylloxera caryaecaulis* the males = 4 autosomes +  $X^I$  +  $X^{II}$ , and the females = 4 autosomes + 2  $X^I$  + 2  $X^{II}$ .)

*Coccidae*: In none of the few forms investigated have sex chromosomes been definitely demonstrated. There is however a possibility that the strange conditions observed in the males of various species of *Pseudococcus* (SCHRADER, '21, '22a) may rest on the fact that half of the chromosomes constitute a compound X and the other half a compound Y (Fig. 32). The males in question have a diploid number of

10 chromosomes. In the meiotic preparatory phases 5 of these condense precociously. No synaptic phenomena are observable. The first spermatocyte division is equational for all 10 chromosomes, but in the second the two groups of chromosomes differentiated earlier by heteropycnosis, pass to opposite poles. The males are evidently heterogametic on this evidence, and that the females are homogametic is borne out by the fact that all 10 chromosomes pair and form tetrads in the maturation of the egg<sup>1</sup>.

*Cercopidae, Cicadidae, Fulgoridae, Jassidae (Cicadellidae), Membracidae:* The sex chromosome condition in all these families is

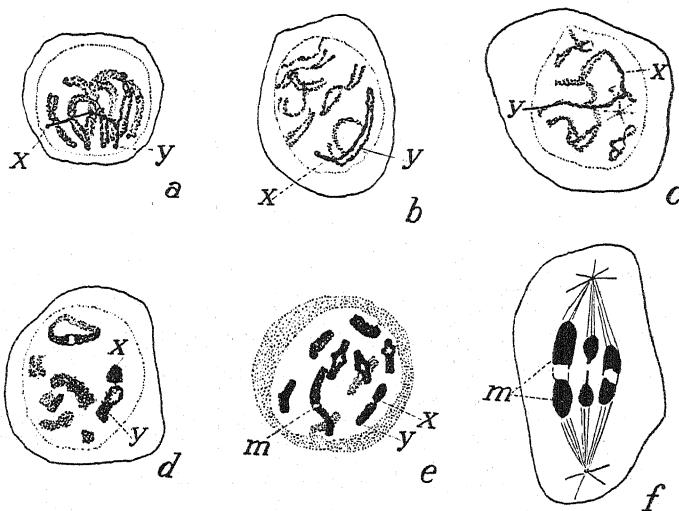


Fig. 33. *Enchenopa binotata* (KORNHAUSER, '14)—*a* Bouquet stage in first spermatocyte, with X and Y joined end to end. *b* Strepsitene stage with X and Y in parasyntapsis. *c* Strepsitene stage showing X and Y separated. *d* & *e* Condensation stages. *f* Side view of first spermatocyte division. *m* = largest pair of autosomes.

of a simple type, with no special complications. The males of the many forms investigated by BORING ('07, '13a, '15) are characterized by an unpaired X which passes undivided to one pole in the first division. The only species in which BORING's account was not clear cut was *Enchenopa binotata*, and there KORNHAUSER ('14) has since demonstrated an XY pair in the male (fig. 33). The behavior of these two sex chromosomes is of some interest especially in the growth stages of the meiosis, both being considerably elongated but staining more intensely than the autosomal threads. During this period also they become united end to end but can be differentiated from each other because of the deeper stain taken by the X. In connection with the question of synapsis it is of significance that the X and Y thread is later bent at the junction of the two chromosomes and these finally come to lie side

<sup>1</sup> These conditions seem to be paralleled in the coccid *Lecanium*, as THOMSEN has recently ('27) pointed out.

## HOMOPTERA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>1. Aphidae</i>						
<i>Aphid</i> from beech	—	8	7 7 + X	—	—	STEVENS '06, '09 b
<i>Aphid</i> from beach golden rod	12 parth.	—	5 5 + X	—	—	STEVENS '06, '09 b
<i>Aphid</i> from <i>Soli-</i> <i>dago altissima</i>	—	6	5 5 + X	—	—	STEVENS '06, '09 b
<i>Aphid</i> from maple	—	16	15 15 + X	—	—	STEVENS '06, '09 b
<i>Aphid</i> (black) from milkweed	8 spg. 8 parth.	4 8 parth.	3 3 + X	—	—	STEVENS '06, '09 b
<i>Aphid</i> from <i>Nasturtium</i>	—	4	3 3 + X	—	—	STEVENS '06, '09 b
<i>Aphis</i> (I) from <i>Oenothera</i> <i>biennis</i>	10 spg. 10 parth.	5 5 ♀ 8 + XX ♂ egg. 10 parth.	4 4 + X	4 4 + X	—	STEVENS '05a, '05 b, '06, '09 b, '10
<i>Aphis</i> (green) from rose	14 parth.	7 14 parth.	6 6 + X	—	—	STEVENS '06, '09 b
<i>Aphis</i> (green) from star cu- cumber	—	5	4 4 + X	—	—	STEVENS '06, '09 b
<i>Aphis</i> (green) from willow (SARANAC)	—	5	4 4 + X	—	—	STEVENS '06, '09 b
<i>Aphis</i> <i>saliceti</i>	5 spg. 5 ♂ soma 6 ♀ soma 6 parth.	3 6 ♀ parth.	2 2 + X	2 + X	—	VON BAEHR '08, '09, '12, '20
<i>Aphis</i> <i>salicola</i>	5 spg.	3	2 2 + X	2 + X	Possibly identical with STEVENS' willow <i>Aphis</i> of HARPS- WELL	STEVENS '06 MORGAN '09 b
<i>Chermes</i> <i>pectinata</i>	20 ♀ soma	10 10 ♀	10	—	Account incomplete	FROLOWA '24
<i>Chermes</i> <i>strobilobius</i>	18—19 ♂ soma 22 ♀ soma, (probably)	10 (=11?) 22 parth. ♀ egg. 20 parth. ♂ egg.	10 or 11 8	—	Account incomplete	FROLOWA '24
<i>Lachnus dentatus</i>	—	4	3 3 + X	—	—	MORGAN '09 b

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Phyllaspis coweni</i>	5 spg. 6 oog.	3	2 2 + X	2 + X	—	MORGAN '15
<i>Phylloxera caryaecaulis</i>	5 (= 6) spg. 6 (= 8) oog.	3 (= 4) 3 (= 4) ♀ 6 (= 8) parth.	3 (= 4) 2 3 (= 4) ♀	3 (= 4) 3 (= 4) ♀ 5 ♂ parth. egg. 6 ♀ parth. egg.	X is composed of 2 components which fuse. Thus ♂ = 4 + X <sup>I</sup> + X <sup>II</sup> ♀ = 4 + X <sup>I</sup> + X <sup>II</sup> + X <sup>II</sup> + X <sup>III</sup>	MORGAN '08, '09 a, '09 b, '12, '15
<i>Phylloxera fallax</i>	10 spg. 12 oog. 12 ♀ soma	6 6 ♀ 12 parth. ♀	4 6 6 ♀	6 6 ♀ 10 ♂ parth. egg. 12 ♀ parth. egg.	♂ = 8 + X <sup>I</sup> + X <sup>II</sup> ♀ = 8 + X <sup>I</sup> + X <sup>I</sup> + X <sup>II</sup> + X <sup>III</sup>	MORGAN '06, '09 b, '12, '15
<i>Stomaphis yanois</i>	—	10	8 + X <sup>I</sup> + X <sup>II</sup> 8	—	All divide in 2nd, but tids from cells with 8 degenerate	HONDA '21

2. *Cercopidae, Cicadidae, Fulgoridae, Jassidae, and Membracidae*

<i>Agallia sanguinolenta</i>	—	11	10 10 + X	—	X divides equationally in 2nd	BORING '07
<i>Amphiscepa bivittata</i>	25 spg.	12 + X	12 12 + X	—	X divides equationally in 2nd	BORING '07
<i>Aphrophora parallela</i>	—	15	14 14 + X	—	—	BORING & FOGLER '15
<i>Aphrophora quadrinotata</i>	—	14	13 13 + X	—	X divides equationally in 2nd	BORING '07 BORING & FOGLER '15
<i>Aphrophora quadrinotata?</i>	23 spg. 23 ♂ soma 24 oog	11 + X	11 11 + X	11 11 + X	—	STEVENS '06
<i>Aphrophora spumaria</i>	—	12	—	—	X to pole in 1st	BORING '13a BORING & FOGLER '15
<i>Atymna castanea</i>	—	11	10 10 + X	—	X divides equationally in 2nd	BORING '07
<i>Campylenchia curvata</i> ( <i>Enchenopa curvata</i> )	19 spg.	9 + X	9 9 + X	9 9 + X	This is the <i>Enchenopa curvata</i> of KORNHAUSER '14	BORING '07 KORNHAUSER '14
<i>Ceresa bubalus</i>	—	11	10 + X 10	—	X divides equationally in 2nd	BORING '07
<i>Ceresa diceros</i>	—	11	10 + X 10	—	X divides equationally in 2nd	BORING '07

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Ceresa taurina</i>	—	10 + X	10 + X 10	—	X divides equationally in 2nd	BORING '07
<i>Chlorotettix unicolor</i>		10 + X	10 + X 10	—	<i>C. unicolor</i> and <i>C. vividus</i> confused. Not known which species has which chromosome conditions	BORING '07
<i>Chlorotettix vividus</i>	21 spg.	8 + X	8 + X 8	—		BORING '07
<i>Cicada (Tibicen) septendicem</i>	19 spg. 20 ♀	9 + X	9 + X 9	—	X divides equationally in 2nd	SCHAFFER '20
<i>Clastoptera obtusa</i>	15 spg.	7 + X	7 + X 7	—	X divides equationally in 2nd	BORING '07 BORING & FOGLER '15
<i>Clastoptera proteus</i>	—	7	—	—	X to pole in 1st	BORING & FOGLER '15
<i>Diedrocephala coccinea</i>	23 spg.	11 + X	11 + X 11	—	X divides equationally in 2nd	BORING '07
<i>Diedrocephala mollices</i>	—	12	11 + X 11	—	X divides equationally in 2nd	BORING '07
<i>Enchenopa binotata</i>	20 spg. 20 oog.	9 + XY	9 + X 9 + Y	9 + X 9 + Y	—	BORING '07 KORNHAUSER '14
<i>Entilia sinuata</i>	21 spg.	10 + X	10 10 + X	—	X divides in 2nd	BORING '07
<i>Lepronia (Aphrophora?) quadrangularis</i>	21 spg.	10 + X	10 10 + X	—	BORING '07 called this <i>Aphrophora</i>	BORING '07, '13 a
<i>Philaenus lineatus</i>	29 spg.	15	14 14 + X	—	—	BORING & FOGLER '15
<i>Philaenus spumarius</i>	23 spg. 23 ♂ soma 24 oog. 24 ♀ soma	12	12 11	—	All chromosomes divide in 2nd	BORING '13 a BORING & FOGLER '15
<i>Phlepsius irroratus</i>	15 spg.	7 + X	7 7 + X	—	2nd division equational for X	BORING '07
<i>Poeciloptera bivittata</i>	—	12 + X	12 12 + X	—	2nd division equational for X	BORING '07
<i>Poeciloptera pruinosa</i>	27 spg. 28 ♀ soma	13 + X	13 13 + X	—	2nd division equational for X	BORING '07
<i>Poeciloptera septentrionalis</i>	27 spg. 28 ♀ soma	13 + X	13 13 + X	—	2nd division equational for X	BORING '07
<i>Thelia bimaculata</i>	21 spg. 21 ♂ soma 22 oog. 22 ♀ soma	10 + X	—	—	X to pole in 1st	KORNHAUSER '14, '19

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Vanduzea arcuata</i>	17 spg.	8 + X	8 8 + X	—	2nd division equational for X	BORING '07
3. <i>Coccidae</i> <i>Pseudococcus citri</i>	10 spg. 10 ♂ soma 10 oog. 10 ♀ soma	10 5	10 5	5 5	Possibly com- pound X of 5 ele- ments and com- pound Y of 5 ele- ments	SCHRADER '23 a
<i>Pseudococcus maritimus</i>	10 ♂ soma 10 ♀ soma 10 oog.	10 5	10 5	5 5	Possibly com- pound X of 5 ele- ments and com- pound Y of 5 ele- ments	SCHRADER '23 a
<i>Pseudococcus nipae</i>	10 spg. 10 ♂ soma 10 oog. 10 ♀ soma	10 5	10 5	5 5	Possibly a com- pound X of 5 ele- ments and com- pound Y of 5 ele- ments	SCHRADER '21, '23 a

by side. But this position is not maintained, for shortly before final condensation, the thread once more becomes straight and in the first division the two sex chromosomes pass to opposite poles.

There are several other species, such as some forms of *Aphrophora*, and *Vanduzea*, where the X although condensing precociously nevertheless becomes considerably elongated in the growth stages of the spermatocytes. In *Campylenchia*, *Philaenus* and several others however it remains rounded and condensed throughout all the preparatory stages. Similar variations are to be observed in the actual divisions. Thus in *Phlepsimus*, the X may precede the autosomes to the pole (in the first division), in *Campylenchia* it lags behind them on the spindle, and in *Vanduzea* it may either precede or lag, both types having been observed in different spermatocytes of the same animal.

But as already stated, the basic conditions as far as the sex chromosomes are concerned, are very uniform. In all cases except one the male has an unpaired X, and it is always in the first spermatocyte division that segregation of the sex chromosomes occurs. Wherever the somatic and oogonial chromosomes of the female have been investigated, the evidence confirms the expectation that 2 X are there present.

As evidence for the fact that the influence exerted by the chromosomes may under certain conditions be overridden, the case of *Thelia* may be mentioned (KORNHAUSER, '19). It was found that males parasitized by the hymenopteron *Aphelopus* may assume certain female characters. Nevertheless at least two such individuals were found in which not only normal testes were present, but which also carried the normal male complement of chromosomes.

## LEPIDOPTERA

As is now well known this is the only group of animals beside that of the birds and perhaps certain fishes in which the females are heterogametic. Superficially then the conditions of sex determination might be expected to be just the reverse of those found in all the other organisms.

This may be indicated by transposing the old designations, so that instead of  $XO$  or  $XY = ♂$ , and  $XX = ♀$ , we would have in birds and *Lepidoptera*  $XO$  or  $XY = ♀$ , and  $XX = ♂$ . However it is not so certain that we are justified in assuming that the sex chromosomes in these special groups are thus equivalent to those encountered elsewhere. For this reason as well as to avoid confusion it seems best to follow the suggestion given by MORGAN and designate the two sexes as follows:

$ZZ = ♂$  and  $WZ$  or  $ZO = ♀$ .

Heterogamety in the female of the *Lepidoptera* was first elucidated from genetic experiments involving sex linkage (as in *Abra*xas by DONCASTER, '08). It is true that MC CLUNG in 1901 mentioned that he had observed in this group as well as in several others an accessory chromosome, but he gave no further evidence to support the claim. Several other cytological investigations of the earlier years carry very little conviction. Thus STEVENS ('06), working on the males of *Cacaecia* and *Euvanessa* reported in the growth stages of the first spermatocyte a bilobed or double chromatin nucleolus which as she thought gave rise to a pair of sex chromosomes. A very similar nucleolus was described by DEDERER ('07) in *Philosamia*, COOK ('10) in *Callosamia* and several other species, and DONCASTER ('11, '12) in *Abra*xas and *Pieris*, all of these investigators regarding this nucleolus as representing an  $XY$  pair present in the males, just as STEVENS had done. In 1914 SEILER pointed out with some justification that the evidence in support of this contention was in every case insufficient and that a similar criticism is applicable to DONCASTER's conclusions in the case of the oogenesis of *Pieris* and *Abra*xas (DONCASTER in 1912 had reported a double nucleolus in the oocytes of these two forms which according to him owed its origin to the condensation of heterochromosomes).

In 1920 DONCASTER himself had come to regard all this earlier cytological evidence on sex chromosomes as of dubious value for he then stated that SEILER in 1913 had been the first to give a cytological demonstration of the sex chromosome conditions in the *Lepidoptera*.

SEILER's accounts of 1913 and 1914 brought out the following conditions in *Phragmatobia* (Fig. 34). In the meiotic preparatory stages of the eggs appears a nucleolus which stains like chromatin. Despite this fact, it does not represent condensed sex chromosomes for it disappears before the metaphase stage of the first maturation division is reached. (A similar observation was made later ('15) by DEDERER in *Philosamia*). The number of chromosomes in this first metaphase plate is 28, and one of these is much larger than any of the other 27. In the division 28 chromosomes go to each pole, but at one of the poles (it

may be in either the polar body group or the group in the egg) the largest chromosome breaks up into 2 smaller chromosomes. Since the second maturation division divides all chromosomes equally, two types of eggs may be formed; if the chromosome which breaks into 2 smaller chromosomes remains in the egg there will be 29 chromosomes, if it is thrown out into the polar body there will be 28 chromosomes.

The diploid number of chromosomes in the male is 56. All sperms are alike and all carry 28 chromosomes.

In SEILER's interpretation, the large chromosome which breaks up into 2 components after the formation of the first polar body in the egg, is a W chromosome (i. e. it corresponds to the Y in cases where

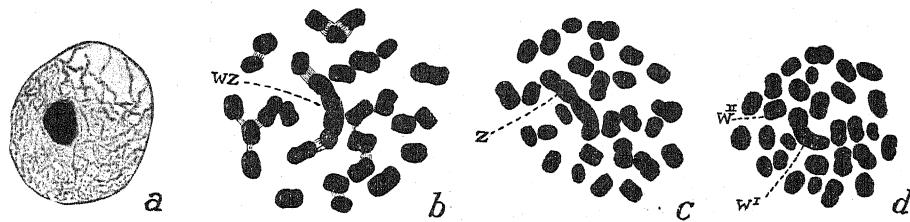


Fig. 34. *Phragmatobia fuliginosa* (SEILER, '14)—a Oocyte in synizesis stage, with true nucleolus. b Metaphase of first oocyte division. c & d Daughter plates of first oocyte division, one including the Z chromosome, the other the two components of the compound W.

males are heterogametic). The Z chromosome (i. e. the X) is slightly larger than the compound Y and in the male is represented twice. As a result of fertilization the following zygotes would be formed:

EGG	SPERM	
$(27 + Z)$	$+ (27 + Z) = 54 + 2Z$	$= 56 = \sigma$
$(27 + W^I + W^II)$	$+ (27 + Z) = 54 + Z + W^I + W^II = 57$	$= \varphi$

Embryos with 56 chromosomes including an equal pair of large ones are indeed found. But the expected type with 57 chromosomes is not present. Instead the remaining embryos usually contain 58 chromosomes and these SEILER attributed to a secondary breaking up of the larger component of the compound W chromosome. This view is supported by the fact that such embryos do not then show the large heterochromosome which is still recognizable by its size after the first fragmentation.

Cases that are more striking because of their greater simplicity were reported by SEILER somewhat later in *Talaeporia* ('17, '19, '20) und *Fumea* ('19, '20). In each case both sexes were investigated and in each the female is characterized by an unmated sex chromosome, so that its sex chromosome formula is ZO.

Mention should be made of the special conditions present in a certain strain of *Abraezus* which DONCASTER discovered and reported in 1913a. In this form both sexes normally have 56 chromosomes, but DONCASTER found some females with only 55. Since these females

## LEPIDOPTERA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Abraxas grossulariata</i>	56 spg. 56 oog. normal race	28 28 ♀	28 28 ♀	—	2nd division equational	DONCASTER '10, '11, '12, '13, '14
	55 oog. ♀ producing race	28 ♀	27 ♀ 28 ♀	—	2nd division equational	
<i>Abraxas laticolor</i>	56 spg. 56 oog.	28 28 ♀	28 28 ♀	—	2nd division equational	DONCASTER '11
<i>Automeris io</i>	—	31	31	—	2nd division equational. 2 equal sex chromosomes?	COOK '10
<i>Cacaecia cerasivorana</i>	—	30	30	—	2 sex chromosomes in male condense precociously	STEVENS '06
<i>Callosamia promethia</i>	38 spg.	19	19	—	2nd division equational. 2 equal sex chromosomes?	COOK '10
<i>Fumea casta</i>	61 & 62 embryos	31	31 30	—	2nd equational for sex chromosomes	SEILER '19, '20
<i>Lycia hirtaria</i>	28 spg. 28 oog.	13 13 ♀	13 14?	—	Male XO?	DONCASTER '13 b
<i>Pieris brassicae</i>	30 spg. probably 30 oog.	15 15 ♀	15	—	2nd equational. 2 sex chromosomes precociously condensed in both sexes?	DONCASTER '12
<i>Philosamia cynthia</i>	26 spg. 26 oog.	13 13 ♀	13 13 ♀	13 13 ♀	2 sex chromosomes in male precociously condensed?	DEDERER '07, '15
<i>Phragmatobia fuliginosa</i>	56 spg. 56, 58, 61, 62 elv.	27 + ZZ 28 ♀	27 + Z 27 + W <sup>I</sup> + W <sup>II</sup> 27 + Z	—	2nd equational for sex chromosomes. W may break up in some soma cells into smaller components	SEILER '14

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Samia cecropia</i>	—	30	30	—	2 sex chromosomes in male condense precociously?	STEVENS '06
<i>Talaeporia tubulosa</i>	60 & 59 embryos	30 30 ♀	29 ♀ 30 ♀ 30 ♂	—	2nd equational for sex chromosomes	SEILER '17, '19, '20
<i>Telea polyphemus</i>	60 spg.	30	30	—	2nd equational. Sex chromosomes?	COOK '10

appeared perfectly normal in every other respect he concluded that the missing chromosome carries few or no factors. The chromosome that would first come under consideration in this connection would of course be the W chromosome (corresponding to the Y of *Drosophila*), DONCASTER further established that in these strains the females gave rise to broods consisting almost entirely of females. The fact that the latter always showed 55 chromosomes led him to the hypothesis that the mothers carrying 55 chromosomes produce eggs in which the now unpaired Z chromosome always goes out into the polar body. This would leave all mature eggs with 27 chromosomes and these when fertilized by the normal sperms (with 27 + Z) would give rise to embryos with 54 autosomes and 1 Z. Such embryos would of course always be females and the whole occurrence could thus be explained. This attractive hypothesis is however not supported by the cytological facts and in a paper published in 1922 after his death, DONCASTER definitely established that 27 chromosomes may go as often into the polar body as 28. His tentative hypothesis that individuals of this strain that contain 56 chromosomes after fertilization have one of the Z chromosomes changed so as to become nonfunctional, is admittedly weak.

Summing up, it appears clear on the basis of genetic evidence and the cytological work done chiefly by SEILER, that in this order of insects the females are heterogametic and the males homogametic. Heterogamety in the females may express itself either as ZO or ZW, but in at least one case it appears that the W as it appears at maturation may be a compound chromosome.

#### ARACHNIDA

As early as 1896 WAGNER described in the spermatogenesis of spiders a "nucleolus" which in the light of later work may be identical with some kind of a heterochromosome. Since that time such chromosomes have been described in a series of species, all of them belonging to the order of *Araneida*. WALLACE in 1900 published an account of

the spermatogenesis in *Agalena naevia* and there described 2 heterochromosomes which she regarded as accessories, i. e. sex chromosomes. She made several corrections of this as well as of a later account ('05) in her paper of 1909, according to which conditions are as follows: There are 2 sex chromosomes in the male, both being components of a compound X. These fuse in the early growth stages of the spermatocytes, but separate again when the autosomal threads undergo synapsis. Only during this latter stage do these heterochromosomes become slightly elongated; at other times they show the form of dense lumps slightly elongated; at other times they show the form of dense lumps. In the first division they pass together to one pole and in the second they divide equationally, but the total number of chromosomes in the spermatids could not be determined with accuracy. WALLACE estimated the latter to be at least 25, but PAINTER ('14) who agreed with the general account as given by WALLACE believed that this estimate is too high.

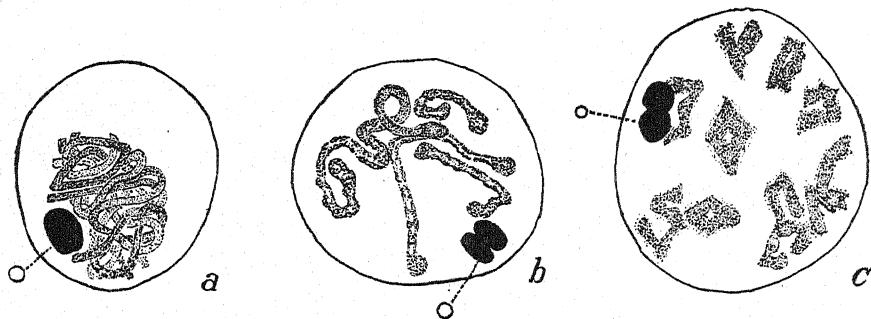


Fig. 35. *Epeira sclopetaria* (BERRY, '06)—a & b Stages in growth period of first spermatocyte showing that there is probably a compound sex chromosome (O). c Condensation stage of first spermatocyte.

MONTGOMERY's description of the spermatogenesis of *Lycosa insopita* ('05) according to which 2 heterochromosomes conjugate in the preparatory phases, pass to opposite poles in the first, and divide equationally in the second spermatocyte division, would lead to the inference that he was dealing with an XY pair. BERRY ('06) on the other hand described a simple XO condition in the males of *Epeira sclopetaria* (Fig. 35).

PAINTER's investigation in 1914 included a reexamination of some genera already described by previous workers. Thus he reported that except for counts of the total numbers of chromosomes, he agreed with WALLACE in regard to the existence of a compound X of 2 components in *Agalena naevia*; he found that his observations on *Lycosa communis* led to the belief that a similar compound X is found there also, and not an XY pair as MONTGOMERY had described in another species of that genus; he confirmed on *Epeira sericata* much of the work reported by Miss BERRY in *Epeira sclopetaria* but concluded that there too there is a compound X of 2 elements and not a simple X as she had found. In fact, he concluded that this condition is probably present in all of the forms that he investigated, so that an  $X^I X^{II} - O$  complex of sex chro-

## ARACHNIDA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Agalena naevia</i>	52 or more, spg.	—	—	25 or more (PAINTER thinks 15)	Unpaired $X^I + X^II$ to one pole in 1st	WALLACE '00, '05, '09 PAINTER '14
<i>Amaurobius sylvestris</i>	—	17	17 16	—	Unpaired $X^I X^II$ to one pole in 1st	PAINTER '14
<i>Anyphaena saltibunda</i>	—	$9 + X^I X^II$	—	—	Unpaired $X^I X^II$ to one pole in 1st	PAINTER '14
<i>Callipes imbecilla</i>	—	$10 + X^I X^II$	—	—	Unpaired $X^I X^II$ to one pole in 1st	PAINTER '14
<i>Chelanops cyaneus</i>	—	$30 + X$	—	—	$X$ to pole in first. May have 2 components	SOKOLOW '26
<i>Dolomedes fontanus</i>	—	$12 + X^I X^II$	—	—	Unpaired $X^I X^II$ to one pole in 1st	PAINTER '14
<i>Dugesiella hentzi</i>	—	$21 + X^I X^II$	—	—	Unpaired $X^I X^II$ to one pole in 1st	PAINTER '14
<i>Epeira scolopetaria</i>	23 spg.	12	11 12	11 12	PAINTER '14 thinks X is com- pound	BERRY '06 PAINTER '14
<i>Epeira sericata</i>	—	—	—	—	Unpaired $X^I X^II$ to one pole in 1st	PAINTER '14
<i>Lycosa communis</i>	—	$10 + X^I X^II$	—	—	Unpaired $X^I X^II$ to one pole in 1st	PAINTER '14
<i>Lycosa insopita</i>	28 spg. (2 counts only)	13	13	—	XY in male?	MONT- GOMERY '05
<i>Maevia vittata</i>	28 spg. 28 ♀ soma	$13 + X^I X^II$	13 13 $+ X^I X^II$	—	—	PAINTER '14
<i>Obisium muscorum</i>	—	$33 + X$	—	—	$X$ to pole in first. May have 2 components	SOKOLOW '26
<i>Oxyopes salticus</i>	—	$10 + X^I X^II$	—	—	Unpaired $X^I + X^II$ to one pole in 1st	PAINTER '14
<i>Xysticus trivittatus</i>	—	$11 + X^I X^II$	—	—	Unpaired $X^I + X^II$ to one pole in 1st	PAINTER '14

mosomes may characterize most males of the *Araneida* and there is some evidence that this may be true also of some Pseudoscorpionidae (SOKOLOW, '26). PAINTER however did not furnish the final check for his conclusions for he gave no account of the oogenesis, while his studies of the diploid phases in the two sexes led to nothing more than estimates of the numbers concerned. The difficulties involved originate in large part in the existence of small chromatin bodies of uncertain character, as well as in so called supernumeraries. PAINTER indeed reached the hypothesis that the interesting occurrence of two morphologically different kinds of male is correlated with differences in these small bodies (ctetosomes) as well as in the supernumeraries.

If therefore it must appear as very probable that the males are heterogametic, and that their sex chromosomes are represented by a compound X without a partner, it must not be forgotten that the final demonstration of this has not yet been made. Beside a study of the oogenesis and the diploid chromosome number, a further analysis of PAINTER's ctetosomes and supernumeraries would be of great interest.

### ECHINODERMATA

A detailed study of the small, threadlike chromosomes of this phylum is made difficult not only because of their great number but also because they are so frequently massed and clumped. The shape of the individual chromosomes is usually that of straight rods of small diameter, but in some species there is also encountered an apparently definite number of V or J shaped chromosomes. Efforts at a study of individual chromosomes have generally been directed at chromosomes of this kind. As has been pointed out, especially by BALTZER ('09), such shapes are due to atelomitic attachment of the spindle fibres.

In 1909 BALTZER described in the cleavage of the echinoid *Paracentrotus (Strongylocentrotus) lividus*, 2 large J shaped chromosomes, and in some cases 1 and in others 2 small J shaped chromosomes—in addition to the usual rod shaped chromosomes. In *Parechinus (Echinus) microtuberculatus* he described 2 large J and either 2 or 3 U shaped chromosomes in different individuals. Fertilized anucleated fragments of the eggs of *Paracentrotus* showed one each of the exceptionally shaped chromosomes, whereas in artificially activated eggs the female pronucleus seemed to show one such chromosome in some cases but not in others. Finally, hybrids from the cross *Parechinus* ♀ and *Paracentrotus* ♂ showed either 1 or 2 U shaped chromosomes. Thus the evidence taken as a whole seemed to show that the female pronucleus may be of two kinds in regard to these exceptionally shaped chromosomes, and if the latter are considered as sex chromosomes it is the female that is heterogametic.

In 1910, HEFFNER stated that in *Lytechinus (Toxopneustes) variegatus* the cleaving, normally fertilized eggs contain either 2 or 3 V shaped chromosomes in addition to the ordinary rod shaped ones. She was unable to trace the unmated V to the female pronucleus, but expressed the opinion that further investigation in this species would support BALTZER's conclusions on sex chromosomes in other echinoids. That there is a chromosomal difference between the two sexes was borne

out further by PINNEY ('11), who found that in embryos from normally fertilized eggs of *Tripterus* (*Hipponoë*) *esculentus*, 17 out of 29 contained a J shaped chromosome which was not present in the others. This investigation did not decide which sex is heterogametic, but in the same year TENNENT threw an entirely new light on the situation. He inseminated *Lytechinus* eggs with *Tripterus* sperms, and found that only half of the hybrids carried the J shaped chromosome seen in normal *Tripterus* embryos. Since HEFFNER had already demonstrated that no such chromosome is to be found in *Lytechinus*, the conclusion seems inescapable that it must have been brought in by half of the *Tripterus* sperms. TENNENT finally pointed out that if the J shaped chromosome really is a sex chromosome, it is the male that is heterogametic for sex and not, as BALTZER had maintained, the female.

TENNENT strengthened his findings in 1912 when he took up the work started by Miss HEFFNER in order to investigate the occurrence of unmated V shaped chromosomes that she had described in the normally fertilized and developing eggs of *Lytechinus*. He found that in fertilized, enucleated egg fragments of this species there are either 1 or 2 V shaped chromosomes, thus demonstrating that here also there are two types of sperms. The case was only made stronger by the fact that eggs artificially activated and therefore developing with only the female set of chromosomes, always showed 2 V shaped chromosomes.

A confirmation of TENNENT's general conclusions finally came from BALTZER himself (1913) who on fertilizing *Sphaerechinus* eggs with *Paracentrotus* sperms discovered that half the embryos carried a J shaped chromosome while the other half did not. Since *Sphaerechinus* carries no such chromosome, it must have been brought by half of the sperms and that finding led to the same conclusion already reached by TENNENT.

TENNENT has recently ('22) published some work which also has a bearing on this point. Normal embryos of *Eucidaris* (*Cidaris*) *tribuloides* (fig. 36) have either 37 or else 38 chromosomes, and corresponding to these two numerical types, there are present either 1 or 2 V shaped chromosomes. Artificially activated eggs, that is eggs with only the maternal chromosomes, usually showed 1 V shaped chromosome, although the evidence on this particular point is not quite conclusive. Hybridization however strengthened the view that the female is homozygous, and the male heterozygous for the chromosome in question. Thus *Eucidaris* eggs inseminated with *Lytechinus* sperms gave embryos with either 2 or 3 V shaped chromosomes. Since the last named species had already been found to carry either 1 or 2 V shaped chromosomes in its sperms, all eggs of *Eucidaris* must be alike in carrying one such chromosome. Similarly, inseminating *Eucidaris* eggs with *Tripterus* sperms, the resultant hybrids were found to have either 3 V plus 1 J shaped chromosome, or else 3 V shaped and no J shaped chromosome. This strengthened not only the view that all eggs of *Eucidaris* carry the same chromosome complement, but also confirmed the older findings that there are two types of *Tripterus* sperms and that these differ only in the presence or absence of a J shaped chromosome.

It should be pointed out that in some forms of Echinodermata, the shape of the chromosomes is not constant under all conditions. For

example the special conditions brought about by hybridization of some form may affect the number of exceptionally shaped chromosomes considerably (HINDERER, '14; LANDAUER, '22). But this only serves to emphasize that each case presents a problem that is more or less independent of all the others.

Despite the difficulties involved in these chromosome investigations, it seems clear that some very definite results have been obtained. Thus there can be little doubt that the two sexes present chromosomal differences in several of the echinoids investigated. Furthermore, whereever

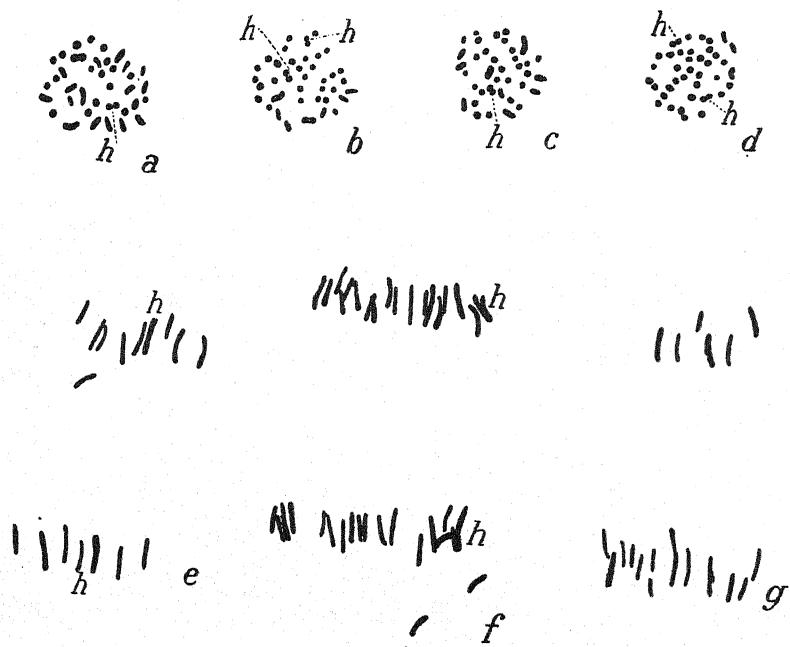


Fig. 36. *Eucidaris tribuloides* (TENNENT, '22)—*a* Polar view of anaphase stage of first cleavage division (37 chromosomes, including one V shaped chromosome). *b* Polar view of first cleavage division (38 chromosomes including two V shaped chromosomes). *c* Same as *a*. *d* Same as *b*. *efg* Three sections of a single figure of first cleavage division involving two V shaped chromosomes. *h* = V shaped chromosome.

a reliable analysis of the chromosomes was feasible, it was the male sex that was found to be heterogametic. In cases like *Eucidaris*, where the male and female have 37 and 38 chromosomes respectively it may be safely assumed that the male has an odd or unmated X, and the female a pair of X chromosomes. If in an instance of this kind it seems justifiable to identify an unmated, exceptionally shaped chromosome in the male as an X, a similar identification of sex chromosomes is not possible in those forms like *Paracentrotus* where according to BALTZER the chromosome number is the same in both sexes. Although in such cases the evidence may make it clear that we are dealing with an XY pair in the male, and though we may possibly be able to recog-

nize the two sex chromosomes as such, the final step of identifying either member of the pair as an X—or a Y, has not been possible so far. It is true that this last step might be taken through a study of the spermatogenesis (as WILSON ('25) suggested), but the technical obstacles to such a study are at present too great.

### ECHINODERMATA

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Cidaris</i> (see <i>Eucidaris</i> )	—	—	—	—	—	—
<i>Echinus</i> (see <i>Parechinus</i> )	—	—	—	—	—	—
<i>Eucidaris tribuloides</i>	37 & 38 clv.	—	—	18 18 + X 18 + X♀	Male is XO	TENNENT '22
<i>Hipponoë</i> (see <i>Triopneustes</i> )	—	—	—	—	—	—
<i>Lytechinus variegatus</i>	36—38 clv.	—	—	18 or 19	Male is XO or XY	HEFFNER '10 PINNEY '11 TENNENT '22
<i>Paracentrotus lividus</i>	36 clv.	—	—	18 prob. 18	Probably XY in male	BALTZER '13
<i>Parechinus microtuberculatus</i> var. <i>bivalens</i>	36 clv.	—	—	—	Probably XY in male	BALTZER '09, '10, '13
<i>Strongylocentrotus</i> (see <i>Paracentrotus</i> )	—	—	—	—	—	—
<i>Toxopneustes</i> (see <i>Lytechinus</i> )	—	—	—	—	—	—
<i>Triopneustes esculenta</i>	32—34 clv.	—	—	—	TENNENT thinks male = XO	PINNEY '11 TENNENT '11, '22

### VERTEBRATA

Up to a comparatively recent period the work done on the chromosomes in this group presented a mass of utter confusion. The astonishing lack of agreement on the simplest and most basic points is well illustrated by the investigations of the chromosomes in man where the diploid number as reported by various workers in over 30 papers varies

from 16 to 48. While there can be little doubt that much of the earlier work on vertebrate chromosomes was superficial and careless, it is only fair to say that the cellular conditions apparently obtaining throughout the group are not favorable to an easy elucidation of the chromosomal conditions. Not only are the numbers exceptionally high (except for some *Marsupialia*), but the unavoidable overlapping of the long chromosomes is complicated by a tendency to clump during many of the crucial stages.

The improved results obtained in the course of more recent investigations are in great part owing to the extreme care with which the material was handled and studied, but also to the use of certain modifications of well known fixing fluids (Modified FLEMMING as elaborated by HANCE, '17a, and Modified BOUIN as used by ALLEN, '19).

Although this most recent work justifies the conclusion that sex chromosomes in vertebrates differ in no essential from sex chromosomes in invertebrates, additional and confirmatory evidence is needed. A few workers like GUTHERZ still seem inclined to doubt that sex chromosomes exist as such in this group, but this view is not shared by the majority of investigators in the field. The cytological evidence, often supported by genetic data, plainly points to the fact that the males are heterogametic in all the included classes except the birds and some fishes, where the females are heterogametic. Moreover the evidence is becoming stronger that in most cases the sex chromosomes of the heterogametic sex are in the form of an unequal XY pair, although in some cases there is still some disagreement on this particular point.

#### PISCES

Genetic evidence obtained by SCHMIDT ('20), WINGE ('22b), and AIDA ('21) established that the males of the species of teleosts they investigated are heterogametic whereas the evidence adduced by BELLAMY ('23) and GORDON ('26) in *Platypoecilus* seems to indicate that there the females are heterogametic. Cytological demonstration of these facts has so far not been given, and that is not surprising since the fishes furnish very unfavorable material for investigations of the chromosomes.

Structures that may possibly represent heterochromosomes were sometimes figured by the earlier investigators in the group, but since in nearly all such cases no further reference was made to them in the accompanying texts, it now seems futile to speculate about them. In 1895 MOORE mentioned a "secondary nucleolus" in the prophases of the meiosis in the males of several Elasmobranchia, but naturally was not aware of its possible significance. WINGE ('22b) in a short paper in which he attempted to give a cytological basis to the genetic results previously obtained on fishes, concluded that in *Lebistes* the males have an XY pair of chromosomes. But as it stands, the account warrants no such conclusion—his evidence being based on the fact that 23 chromosomes show in both spermatocyte divisions, that the oogonia carry 46 chromosomes (although one of his figures shows 45), and that in the diakinesis of the first oocyte there are 23 pairs or tetrads (this number based on a cell cut into three sections). There appears to be no heteropycnosis,

no lagging or precession, or any other feature which might suggest the presence of heterochromosomes of any kind. It is plain that without some such indication, the rather doubtful findings that the number of chromosomes is the same in both sexes can not be regarded as a cytological proof of the presence of an XY in the male.

FOLEY's description of spermatogenesis in *Umbra* ('26) parallels that of WINGE in that no trace of any special behavior on part of any of the chromosomes could be discovered. FOLEY suggested that a large pair of L shaped chromosomes may represent sex chromosomes and then proceeded to the conclusion that in that case the male must have a pair of X chromosomes, but it is manifestly useless to consider this suggestion seriously without additional evidence. Again, GEISER ('24) expresses the opinion that in *Gambusia* males the presence of sex chromosomes is indicated, but advances no real support for this hypothesis.

#### AMPHIBIA

The great amount of work that has been done on the cytology of this group has not cleared up the question of the sex chromosomes nor the apparently complicated conditions underlying the more general aspects of sex determination.

H. D. KING ('12) has published what appears to be the only paper specifically concerned with sex chromosomes in the Urodela. She concluded that in the males of *Necturus* an X chromosome is attached more or less constantly to one of the autosomal tetrads and passes undivided to one pole in the first division. Miss KING holds it possible that a smaller Y may also be attached to the autosomal bivalent in question. The second division appears to present some difficulties to a successful analysis, although Miss KING is inclined to believe that the X then divides equationally. Unfortunately her promised further investigation of the question, especially in regard to the Y, has never appeared, and PARMENTER's suggestion ('19) that similar conditions may obtain in *Ambystoma* is too indefinite to throw any further light on the sex chromosomes of the Urodela.

In the Anura it has been a question for some time as to whether the male or the female is heterogametic. The fact that frogs from artificially activated eggs may be of either sex gave support to the hypothesis that the female is heterogametic. However if WITSCHI's results ('23) obtained in breeding experiments involving an hermaphrodite frog can be confirmed, little doubt is possible that it is the male that is heterogametic.

The purely cytological evidence is not decisive. LEVY ('15) in work that has never been confirmed by any worker since then, reached the conclusion that the males of *Rana esculenta* have an unpaired X which in the first spermatocyte division passes undivided to either pole. SWINGLE ('17) reached a similar conclusion in *Rana pipiens* but retracted these findings in 1921, concluding that the X of his earlier paper had been an ordinary autosome. Indeed it now seems fairly certain that the male frogs have an even number of chromosomes and that this number is the same as that found in the females, so that it seems safe to conclude that a simple XO condition can not be present.

The recent work of WITSCHI ('24) is an endeavor to elucidate this point in *Rana temporaria* (fig. 37). The spermatogonial number in that species is 26. In the first spermatocyte plate are found 13 elements and the largest of these divides before the others. The division is however equational, and 13 chromosomes go to each pole. The largest at this time betrays a compound constitution through a marked constriction giving it a bilobed appearance. In the second division this chromosome is divided, the larger lobe going to one pole and the smaller to the other. Usually it shows a distinct tendency to lag on the spindle at this time. WITSCHI concluded that we have here an unequal XY pair, of which the larger component represents the X. The case presents some difficulties however. Aside from the fact that identification of either member of the pair as the X does not seem possible without examination of the chromosomes in the female, the difference in size between the chromosomes in question is so small, that even if female chromosome plates become available, a final decision may well be impossible. Indeed aside from the precession in the first and lagging in the second division, little supporting evidence is available for the hypothesis that we are dealing with sex chromosomes at all. Recognizing the care with which WITSCHI's work was performed, it nevertheless seems advisable to defer a final conclusion on the question of the sex chromosomes in frogs.

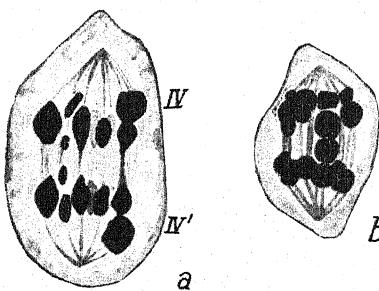


Fig. 37. *Rana temporaria* (WITSCHI, '24)  
—a Anaphase of first spermatocyte division showing double structure of what are probably the fused sex chromosomes.  
b Anaphase of second spermatocyte division, showing the supposed XY pair lagging on the spindle. IV & IV' = sex chromosomes.

REPTILIA

Until 1919 the only work on sex chromosomes in this class of vertebrates was reported by JORDAN ('14a) who found in the males of two species of the Chelonia a bipartite body that he suspected of being identical with sex chromosomes. In view of the phylogenetic relationship between reptiles and birds and the fact that in the latter there had long been genetic evidence for the belief that the female is heterogametic, a cytological analysis of both classes has always been of great interest. In the year mentioned above, DALQ reported on the spermatogenesis of *Anguis*, one of the Lacertilia, and his work showed that generally speaking the chromosomal conditions in the two classes are very much alike especially in the fact that there is a number of very small chromosomes (microchromosomes) in addition to some of a more ordinary size (macrochromosomes). The former type of chromosome opposed great difficulties to an exact cytological analysis but DALQ was able to arrive at more definite conclusions in regard to the macrochromosomes. He found that in the diploid sets they always number 19,

that after pseudoreduction there are always 10 of them, and that in the first spermatocyte division one of these 10 passes undivided to one of the poles. Since the second division is equational the indications are plain that the male has the XO condition. But it must not be forgotten that the behavior of the microchromosomes is not certain. These observations agree fairly well with those of PAINTER (fig. 38) which were published in 1919 and 1921. The great differences in the number of diploid chromosomes reported by the two observers is no doubt to be attributed to the fact that they worked on different families

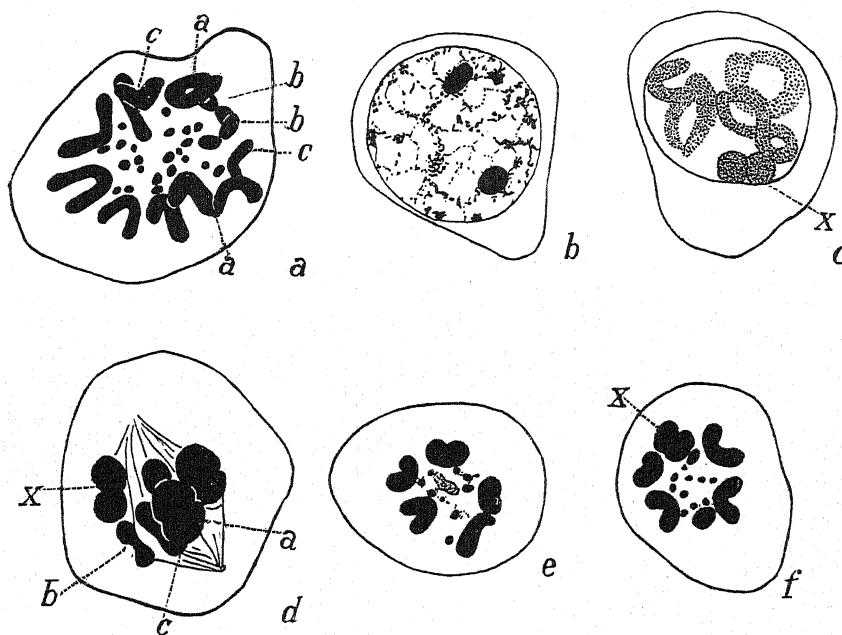


Fig. 38. *Anolis carolinensis* (PAINTER, '21 a)—*a* Spermatogonial metaphase plate. *b* Preleptotene stage of first spermatocyte, showing two chromatin nucleoli. *c* Prophase with two condensed sex chromosomes. *d* First spermatocyte division, showing precession of compound X. *e* Metaphase of second spermatocyte with 5 large chromosomes. *f* Metaphase of second spermatocyte showing 6 large chromosomes, including the fused components of the compound X.

of lizards. A more significant difference lies in the observation made by PAINTER that in the first spermatocyte metaphases there is always a bipartite body which takes its origin in the union of 2 chromosome nucleoli during the prophases, goes undivided to one pole in the first division, and divides equationally in the second. The bipartite body appears to break up into 2 separate chromosomes in the somatic and spermatogonial cells, and thus behaves like a compound and multiple sex chromosome. The belief that we are really dealing here with an unpaired  $X^I X^{II}$  in the male is made more certain by the fact that diploid counts in the female show 2 macrochromosomes more than in the males. PAINTER like DALCQ experienced difficulty in studying the

microchromosomes, but he is of the opinion that they behave like typical autosomes.

In the Ophidia there is available only THATCHER's fragmentary preliminary report on the spermatogenesis of *Thamnophis*. Again macro- and microchromosomes are encountered. THATCHER is not quite certain of the spermatogonial counts, but in the first spermatocytes finds 17 autosomal elements and a tripartite body. The latter in the first division divides so that one of its components goes to one pole and the remaining two to the other. It is THATCHER's opinion that he is dealing with a compound X of 2 components and a Y, but he gives no other supporting evidence for this conclusion, having made no counts of the chromosomes in the cells of the female.

Peculiar interest lies in the conditions which obtain in the primitive reptile *Sphenodon*. The only account is that of HOGBEN ('21) who unfortunately was unable to determine accurately the numbers of chromosomes and also stated that "there was no sign of an accessory element in the material at my disposal". It is needless to say that HOGBEN'S evidence does not settle the question of sex chromosomes in this form.

Taking the group as a whole, the evidence seems clear that the males are heterogametic and not the females (as in the birds), although it still seems desirable that the behavior of the microchromosomes be studied more exactly.

#### AVES

Indications are that in this class also the modern cytological methods will soon clear up the question of sex chromosomes. The pioneer in the field was GUYER who in two papers ('09 a & b) on the spermatogenesis of the guinea (*Numidia*) and the chicken (*Gallus*) respectively, reported the discovery of an unpaired sex chromosome. In *Numidia* the diploid number as represented by the spermatogonia was given as 17, whereas the number in *Gallus* was between 15 and 19. In both cases 9 elements (8 bivalents + X) were found in the first spermatocyte, and in the first division the sex chromosome was described as going undivided to one pole. The secondary spermatocytes thus received either 8 or 9 chromosomes, but due to a secondary pairing only 4 and 5 bodies appear there. The second division is equational, so that two types of sperms are finally formed, and GUYER believed that these two types can be distinguished also on the basis of size.

GUYER's evidence thus indicated that in the birds as in so many other animals, the males are heterogametic. However the results of breeding experiments a short time after showed plainly that it is the female and not the male that is heterogametic in this class. This was pointed out by BORING and PEARL ('14) who in their cytological investigation of *Gallus* were unable to confirm GUYER's findings in regard to the X chromosome in the male. In 1916 GUYER published another account of the spermatogenesis of the chicken and made the following corrections: The unpaired X he now regarded as a double element, i. e. composed of 2 chromosomes. Somatic cells showed that these 2 chromosomes are there separated. The spermatids with only 4 chromosomes degenerate, and only those with 5 form normal sperms. Finally, he

retracted his conclusions on the different sizes of sperm and now stated that only one type is found.

It is clear that with these corrections, the evidence would indicate that the males are homogametic. With all due respect to the difficulties of pioneer work, this later work of GUYER gives the impression that was somewhat brusquely expressed by P. HERTWIG ('23): "Die Arbeit macht sehr den Eindruck, als sollten die Beobachtungen in der ersten Veröffentlichung mit den Forderungen der Genetik in Einklang gebracht werden."

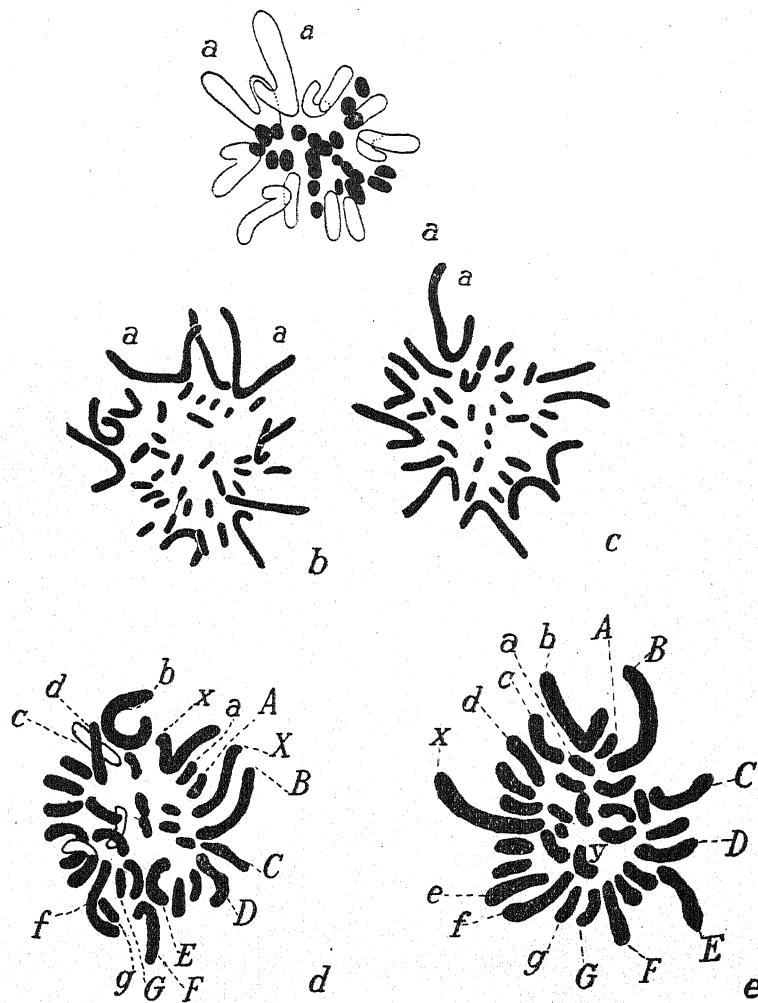


Fig. 39. *Gallus gallus* dom. (BORING, '23)—a Miss STEVENS figure of spermatogonial plate with two large chromosomes (a). (HANCE, '24) b Somatic plate of male, with two large chromosomes (a). c HANCE's figure of somatic plate of female, with only one large chromosome (a). (SHIWAGO, '24)—d Diploid chromosome complex of male, including 2 X (or 2 Z). e Diploid chromosome complex of female, including X and Y (or Z and W).

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Both GUYER's and BORING and PEARL's investigations plainly indicated that the technique employed was inadequate for the solution of the problem. A recent note by BORING ('23) however brings the surprising evidence that as early as 1912 Miss STEVENS had made a study of the chromosomes of the chicken and that her results were very close to our more modern findings. Her drawings of the spermatogonia show 12 large chromosomes and 20 or more very small ones (fig. 39 a). In the first spermatocytes there are usually figured 6 large and 12 to 14 small chromosomes. In addition to these differences in chromosome counts, STEVENS apparently also disagreed with GUYER in having been unable to find a secondary pairing prior to the second spermatocyte division (noted by BORING and PEARL, '14).

HANCE ('24) reported that he had found 35 to 40 chromosomes in the somatic cells of the chicken (fig. 39 b & c) and SHIWAGO ('24) reported 32 (fig. 39 d & e). (It may be remarked here that GUYER ('16) in his fig. 88 shows 33,—without comment.) It is to be noted that both STEVENS and HANCE give figures very reminescent of the chromosome conditions in reptiles in that beside several larger chromosomes there are some very small chromosomes, but that point is not so striking in SHIWAGO's figures. But more significant in the present discussion is the fact that both HANCE and SHIWAGO found, as had Miss STEVENS, that in the males the 2 largest chromosomes form a pair, whereas in the females (on which Miss STEVENS did not work) the largest chromosome—corresponding in size and form to the large ones of the male—has no equal partner. Regardless of whether the largest chromosome in the female has a partner (as SHIWAGO claims), the agreement among the different workers on one fact is definite,—the males are homozygous and the females heterozygous for the largest chromosome. Plainly therefore the indications are that the female is heterogametic, although just as in the reptiles a further study of the smaller chromosomes is called for before we can arrive at a final conclusion<sup>1</sup>.

#### MAMMALIA

So much confusing and contradictory work has been published on the chromosomes of the mammalia that a consideration of the different families in which sex chromosomes have been reported seems warranted.

#### MARSUPIALIA

In several respects the marsupials are more favorable for a study of the chromosomes than any of the other mammals. Already in 1906 BENDA described in the male of *Parameles* a "nucleolus" and an "intranuclear body". His interpretation is not quite clear and GUTHERZ ('22) later was of the opinion that BENDA had been mistaken in his identification of these two inclusions. In 1911 JORDAN reported that he had found the XO conditions in the males of the opossum (*Didelphis virginiana*), but more recent accounts show that JORDAN was in error

<sup>1</sup> AKKERINGA ('27) has just reported 32 as the spermatogonial number. However, as far as the sex chromosomes are concerned neither his nor HANCE's most recent paper ('26) adds anything essential to the above conclusions.

in this as in several other respects. Thus HARTMANN ('19) showed that in the maturation of the egg the haploid number of chromosomes indicates the fact that JORDAN's estimates of the diploid number in the male had been too low. This was followed by a careful analysis of the chromosomes in both sexes by PAINTER ('21b, '22a, '24a) who showed

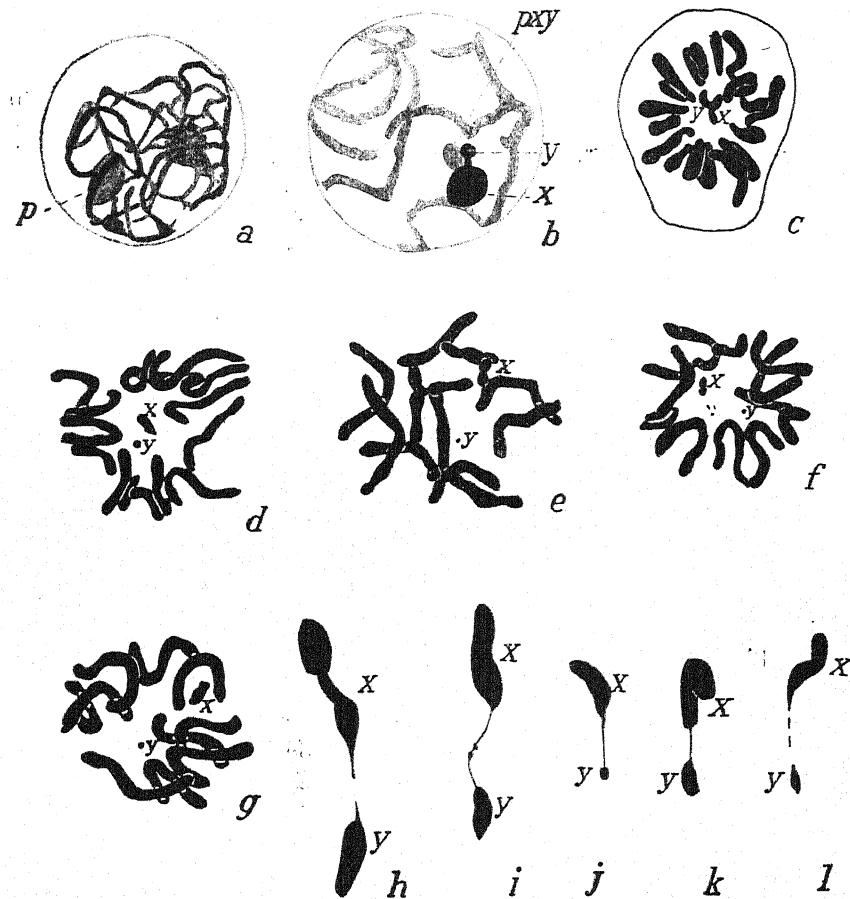


Fig. 40. *Macropus ualabatus* (AGAR, '23)—*a* Synthesis stage of first spermatocyte, showing no heteropycnosis. *b* Late pachytene stage of first spermatocyte, showing condensed XY pair and attached plasmosome (pxy). (PAINTER, '25 b, following AGAR, '23 and GREENWOOD, '23 in *d, e, f & g*)—Spermatogonial plates of *c* *Didelphis*, *d* *Phascogale*, *e* *Sarcophilus*, *f* *Dasycercus*, *g* *Macropus*. Sex chromosomes in the male of *h* *Didelphis*. *i* *Homo*. *j* *Macacus*. *k* *Cebus*. *l* *Equus*.

that the diploid number is always 22, and that the male has an unequal XY pair the members of which pass to opposite poles in the first division and constitute the smallest chromosomes in the set (fig. 12).

AGAR ('23) and several of his students (GREENWOOD, '23, ALTMANN & ELLERY, '25) found some rather favorable material in a number of Australian marsupials (fig. 40). The numbers of chromosomes are

small as compared with those found in other classes of mammals, the males always have the XY condition, segregation of the sex chromosomes always takes place in the first division, and a study of female cells always shows the larger of the unequal pair of sex chromosomes to be the X.

Only on some minor points do the Australian workers differ with PAINTER. Thus the latter reported the appearance of 2 chromatin nucleoli (which later give rise to sex chromosomes) already in the resting stage of the first spermatocytes, whereas AGAR believes that a single chromatin nucleolus gives rise to both of the chromosomes in question and that this nucleolus does not definitely appear until the pachytene stage. Again, PAINTER described a plasmosome (fig. 12) which he believes to be entirely independent of the sex chromosomes, whereas both AGAR and GREENWOOD found plasmosomes at least one of which is formed from the condensing sex chromosomes. But aside from this, these recent investigations agree that it is the male that is heterogametic, and that this condition is expressed through an unequal XY pair.

#### EDENTATA

In 1910, NEWMAN and PATTERSON reported in the armadillo, *Tatu novemcinctum*, 31 and 32 as the diploid numbers of the male and female respectively. The odd number in the male as well as the behavior of an apparently unpaired chromosome during the spermatocyte division led them to the conclusion that the male has sex chromosomes of the XO type. Oddly enough, NEWMAN two years later discussed the possibility of a heterochromosome in the female (having found a plasmosome like body in the oocytes), apparently disregarding the earlier account. But both of these earlier papers appear erroneous in the light of PAINTER's (25a & b) preliminary studies on the same animal. These seem to show that both sexes have 60 chromosomes for the diploid number (as shown in amnion cells), and therefore it is more likely that the XY condition will be found in the heterogametic sex.

#### UNGULATA

*Bos*: WODSEDALEK's account ('20) gives the spermatogonial number as 37, one of these being distinctly larger than the others and regarded by him as an X. After pseudoreduction there are 18 bivalents + 1 heart-shaped univalent (the X). The latter passes undivided to one pole in the first spermatocyte division and divides equationally in the second (fig. 41). The female has 38 chromosomes, two of them being X chromosomes of the same shape as that of the single X in the male. According to WODSEDALEK, these two X chromosomes condense precociously in the oocyte prophases just like the single X in the corresponding phases of the spermatogenesis. It is worthy of note that WODSEDALEK reports here as he had for other mammals in earlier papers, that there is a tendency toward a second pairing of chromosomes after the first spermatocyte division—a point that has long been under dispute. The account of MASUI ('19b) differs from the preceding in several ways. According to MASUI the spermatogonia show 33 chromosomes including a single

unpaired X, and there is no second pairing. Unfortunately, there is only one other account of the chromosomes in cattle. That, published in 1901, is by SCHOENFELD who mentions and figures a nuclear inclusion in the spermatogenesis which he calls "corpuscle intra-nucléaire". The nature of this body is however not clear. The evidence as given by WODSEDALEK and MASUI indicates that the male is heterogametic and has the XO type of sex chromosomes.

*Equus*: The figures given by KIRILLOW ('12) indicate the presence of a chromosome nucleolus in the spermatocyte prophases, but this investigator does not consider its possible significance. JORDAN ('11, '12, '14b) however described two such bodies which later in the prophases come together to form a bilobed or trilobed X element. In contrast with this account, WODSEDALEK ('14) described an X that arises

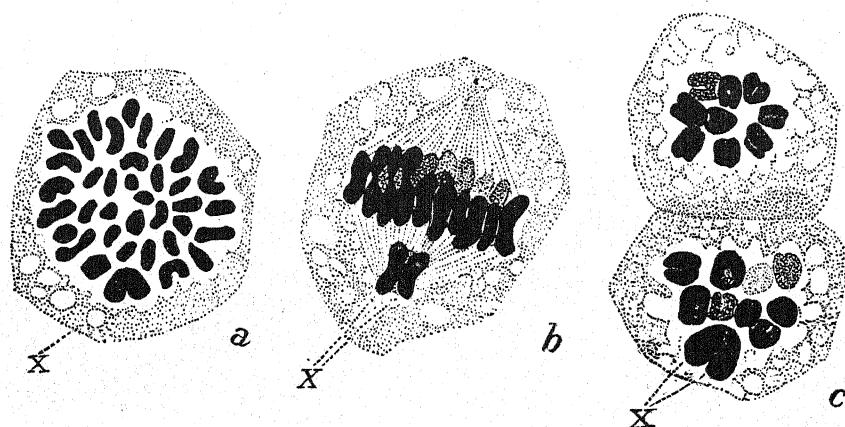


Fig. 41. *Bos* (WODSEDALEK, '20)—a Spermatogonial metaphase showing heartshaped sex chromosome. b First spermatocyte division showing split sex chromosome. c Metaphase of second spermatocyte after the so called second pairing.

from a single chromosome nucleolus. In the first spermatocyte division it passes undivided to one pole while in the second it divides equationally. WODSEDALEK's account receives some confirmation through his own study of the spermatogenesis of the mule ('16) as well as from MASUI's account ('19a) of the spermatogenesis in the horse. In the mule (a hybrid from the cross of *Equus* by *Asinus*) WODSEDALEK believed he could recognize the X, similar in shape to that of the horse, in both the spermatogonia and the spermatocytes. MASUI confirmed not only the presence of an unpaired X in the male of *Equus*, but also arrived at the same counts of chromosomes in the first spermatocytes, namely 18 bivalents + 1 X. Despite this, PAINTER ('24c) in a very conservative account of the spermatogenesis concluded that previous observers had underestimated the diploid number of chromosomes in the horse, and that this number is much closer to 60 than to 37 as given by WODSEDALEK. Again in the first spermatocyte PAINTER found 30 instead of the 19 elements reported by WODSEDALEK and MASUI. His more detailed study points to the presence in the male of an unequal

XY pair, whose members separate and pass to opposite poles in the first spermatocyte division. PAINTER's criticism that the technique employed by previous workers had been inadequate for an accurate determination of the conditions seems justified by a comparison of the figures given by them and by himself. But since PAINTER's own study is admittedly not entirely complete, a conclusion in regard to sex chromosomes can not be reached. The chances are that PAINTER is correct in his hypothesis that here as in many other mammals investigated by him, the male has an unequal XY pair.

*Ovis:* For the sheep we have only JORDAN's brief description ('14b) in which he recognizes an X element in the male, tracing it through the preparatory phases of the first spermatocyte. Obviously, his account does not justify any conclusion.

*Sus:* As far as sex chromosomes are concerned, WODSEDALEK's two papers of 1913 represent the only attempt at a complete account. According to these, the diploid number as present in the spermatogonia, is 18. Of these 2 are sex chromosomes, that is, the X is a compound of 2 components. The autosomes form 8 bivalents in the metaphase of the first spermatocyte division and these divide normally while the 2 X components pass undivided to one pole. Thus the second spermatocytes are of two types, 8 and  $8 + X^I + X^{II}$ . But WODSEDALEK reported that there is a second pairing at this time with the result that the second spermatocytes finally show either 4 elements or 6 elements (the latter including the 2 X components). The final division is equational for the sex chromosomes. JORDAN ('14b) commenting on WODSEDALEK's work stated that "my material does not confirm his findings that two large round nucleoli remain very conspicuous throughout the process of growth of the primary spermatocytes", but in general seemed ready enough to abandon his own belief that no sex chromosomes are found in the pig. Therefore as matters then stood, the male pig would be heterogametic and have an unpaired compound X of two components. But in the light of more recent evidence published by HANCE ('17b), this conclusion can not be considered as final. HANCE found the spermatogonial number to be 40, while the first spermatocytes showed 20. In view of the careful technique employed by HANCE a reconsideration of the question is called for, since if WODSEDALEK actually erred in his counts as much as HANCE's figures would indicate, very little reliance could be placed on the rest of his account.

#### CARNIVORA

*Canis:* MALONE ('18) working on several kinds of domestic dogs reported 21 chromosomes in the spermatogonia, of which he considered one as an unpaired X. After pseudoreduction he observed 10 bivalents and the unpaired X, the latter passing undivided to one pole in the first meiotic division and dividing equationally in the second. Confirmatory evidence was found in the counts of the chromosomes in the female which show 22 as the diploid number. MALONE's figures show more or less clumping of the chromosomes and his findings should not be regarded as final, especially if PAINTER ('25b) is correct in reporting that the diploid number is really very close to 50 and probably 52.

*Felis*: A good deal of discussion has been based on the announcement of VON WINIWARTER and SAINMONT ('09) that an unpaired heterochromosome is to be observed in the oogenesis of the cat. LONGLEY ('11) and VAN DER STRICHT ('11) were unable to confirm this finding and in 1914 VON WINIWARTER modified the earlier account by interpreting the body in question as formed by the union of 2 heterochromosomes. At the same time he described an unpaired X in the male and thus supported an earlier account of VEJDOWSKY ('09). But GUTHERZ in a series of publications not only opposed VON WINIWARTER's first conclusions in regard to the female, but also expressed doubt as to his interpretation of the intranuclear body in the male as a sex chromosome ('12, '18a, '18b, '20). GUTHERZ gains some doubtful support from the early description of LOEWENTHAL ('88). The uncertainty in the status of the problem even now is illustrated by the fact that the diploid number of chromosomes was given by VON WINIWARTER as 36, by GUTHERZ as 38 (in his most recent publication of 1925 he seems inclined to accept slightly higher counts), and by HANCE ('17a) as close to 50 (as shown in a drawing). The question of sex chromosomes in the cat must therefore be regarded as unsettled.

*Herpestes*: JORDAN ('14b) could find no sex chromosome in the male of the mongoose.

#### RODENTIA

A great deal of work has been done on the chromosomes of this group of mammals, although much of it has no direct bearing on the presence and nature of sex chromosomes. Many of the earlier observers described or figured in the preparatory phases of the spermatocytes the body which later was called "intranuclear body" or "chromosome nucleolus". Thus SANFELICE ('88), LENHOSSEK ('98), LA VALETTE ST. GEORGE ('98), DUESBERG ('08), and REGAUD ('10) may all have seen this body. REGAUD and ALLEN ('18) believed that VON EBENER ('88) had described the intranuclear body prior to any of the workers mentioned, but aside from the fact that his figures present no convincing evidence that he really made the observation, he himself ('99) stated that he had overlooked it in his earlier paper. LUKJANOW ('98) described an unequal distribution of chromosomes in the first spermatocyte division of the mouse, but it seems possible that he may have made his observations on abnormal cells. The possible relation of such a heterokinesis to sex determination was not recognized by LUKJANOW and it was left to McCLUNG to suggest that the accessory-like body which he had seen in the mouse is identical with a similar body in insects where it has a distinct influence on sex determination. McCLUNG however did not go beyond the mere mention of this possibility as far as the mouse was concerned and published no description of the body in question. Again, like GUYER ('10) who claimed to have found a corresponding chromosome in the spermatogenesis of the rat, he neglected to consider its relationship to the intranuclear body which had been described by other observers in the preparatory phases. VEJDOWSKY ('09) seems to have been the first to point out that these bodies, one seen in division and the other in preparatory phases, are possibly identical.

*Mus*: It is difficult to decide just how accurate the observations of the earlier workers just mentioned were. Indeed as far as the mouse is concerned, the question of sex chromosomes is not settled even now. JORDAN ('14b) described a heterochromosome in the male of *Mus musculus* and suggested that it might be a double accessory, although he was not certain of its behavior during the meiotic divisions. YOCOM ('17) like JORDAN found a chromatin body in the prophases of the spermatocytes. In metaphases of the first spermatocyte he counted 20 elements, one of which he regarded as an unpaired X derived from the chromatin body already mentioned. This sex chromosome he described as dividing equationally in the first and passing undivided to one pole in the second division, so that the resulting sperms carry either 18 or  $18 + X$ . But some of the figures given by YOCOM do not support his account of the meiotic divisions. Thus his fig. 3, of the first spermatocyte division, may easily be interpreted as showing the X passing undivided to one pole, while his fig. 8, supposedly of the second division, does not at all demonstrate reductional division of the sex chromosome. In short, YOCOM's account is not convincing. GUTHERZ ('22) working on the white mouse, concluded that the intranuclear body as it appears in the growth stages of the spermatocytes does indeed give rise to a chromosomal body in the first metaphase. But this body according to him does not represent a sex chromosome but an autosomal tetrad. This conclusion has not gone without a challenge and PAINTER ('24a) argued that GUTHERZ's evidence on the actual division stages is entirely insufficient for such an interpretation. Finally may be mentioned MASUI's account ('23) according to which the males have 40 chromosomes, including 2 sex chromosomes. MASUI did not make a complete analysis of the divisions but believed that this pair of sex chromosomes represents an X and a Y. This conclusion was also reached by Miss COX ('26).

In the male of *Mus sylvaticus*, FEDERLEY ('19) like GUTHERZ in the case of the house mouse, concluded that the intranuclear body of the growth stages is identical with a heterochromosome, but hesitated to commit himself on its exact nature.

In the white rat, ALLEN ('18) described an unpaired X which makes its first appearance during meiosis in the leptotene stage of the first spermatocyte. In the metaphase it shows a split but passes undivided to one pole in this division whereas the second division is equational. ALLEN's conclusion that sperms with 18 and  $18 + X$  are formed agrees with YOCOM's conclusions in regard to the house mouse. More recently RAU ('25) concluded that the rat has a diploid number of 40. LONG and MARK's work on the maturation of the egg ('11), which supported TAFANI's earlier count ('89) of 20 as the haploid number in the egg of the mouse finally makes it seem certain that all these counts are very nearly correct. But the status of the sex chromosomes is not clear.

*Lepus*: BACHHUBER ('16) without referring to JORDAN's ('14b) earlier negative evidence, reported that in the prophase of the first spermatocyte 2 chromatin nucleoli are distinguishable—usually close together. He interpreted these as an X and a Y, and believed that they pass to opposite poles in the first division. Although BACHHUBER is in general supported by the more recent findings of PAINTER ('25a & b,

'26), MASUI has reported an unpaired X in the male. Indeed it is not quite certain that his material justified his conclusions. Thus he gave the diploid number as 22 whereas PAINTER reported 44 and MASUI 47 chromosomes in the male. Therefore while the indications point to heterogamety of the male, no final analysis has yet been made.

*Sciurus*: Figures given by VAN MOLLE in his account of the spermatogenesis of the squirrel show no trace of a heterochromosome. JORDAN ('14b) who was specifically looking for sex chromosomes was also unable to demonstrate them in the male. However neither account justifies any conclusion in regard to these chromosomes.

*Cavia*: STEVENS ('11b & c) described 2 chromatin nucleoli in the prophase stages of the spermatocytes. She regarded these as the X and Y respectively and found that they passed to opposite poles in the first division. The interkinesis shows two types of cells, one having a large and the other a small chromatin nucleolus, and these again represent the X and Y. The material proved unsatisfactory for a study of the second spermatocyte division but although the evidence is thus not complete, it is probable that Miss STEVENS was correct in ascribing an XY pair of sex chromosomes to the male of the guinea pig. HARMAN and ROOT ('26) have recently reached a similar conclusion in regard to the sex chromosomes, but their figures are hardly conducive to confidence in their interpretations.

#### CHIROPTERA

In the prophases of the spermatocytes of the bat (probably *Vesperugo*) JORDAN ('12) described a chromatin nucleolus which can be traced to the first metaphase. At that time it becomes indistinguishable from the autosomes. JORDAN considered the possibility that he was dealing with a sex chromosome less highly differentiated than in those cases where it can be easily traced through the meiosis. His estimate of the diploid number of chromosomes as at least 24 does not compare favorably with the count given more recently by PAINTER ('25a & b) who reported a diploid number of 48 for *Nyctinomous mexicanus*. But it is of course likely that this difference may be due to the fact that different species are concerned. PAINTER suggests that since all embryos carry this even number, it is likely that the males will be found to have an XY pair. The high number of chromosomes found by PAINTER finds some confirmation in the figure of the chromosomes of a bat (species not given) showing at least 40 chromosomes, given by HANCE ('17a).

#### PRIMATES

It appears that PAINTER's investigations ('22b, '23b, '24b) represent the only work on the sex chromosomes in the lower Anthropoidea. In the males of what PAINTER calls the brown *Cebus* of South America the diploid number of chromosomes is given as 54. In the growth stages of the primary spermatocytes a chromatin nucleolus was observed, but not completely analyzed. 27 bivalent elements are found in the first spermatocyte metaphase and one of these stains less intensely than the others and is distinguished moreover by the inequality in size of

its two components. The latter separate and pass to opposite poles in the first division. A detailed study of the second division was not possible.

In the males of the old world monkey *Rhesus maccacus*, the diploid number is 48, but the other main features of its spermatogenesis are identical with those given for the brown *Cebus*. Here PAINTER was able to study the diploid group of chromosomes in the female and found it to be composed of 48 with the small component of the unequal pair not present. In both forms it therefore appears likely that the males are heterogametic and have an unequal XY pair of sex chromosomes.

*Homo*: As might be expected a great deal of work has been reported on the chromosomes of the human being. No analysis of all these investigations is intended here except as they may bear on the question of the sex chromosomes. The first account taking up that aspect was published by GUYER ('10) who described 20 autosomes and an X of 2 components in the spermatogonia. In the first spermatocyte these two X components pass undivided to the same pole while in the second they divide equationally. Finally there are two types of spermatids, one containing 2 chromatin nucleoli and the other none. By inference then the female would carry a diploid set of 24 chromosomes ( $20 + 2 X^I + 2 X^{II}$ ).

GUTHERZ ('12) like GUYER reported 2 heterochromosomes in the male but concluded that they did not represent sex chromosomes but merely a pair of autosomes that for some unknown reason undergo heteropycnosis in meiosis. GUTHERZ's attitude on this point has been consistently maintained by him and he has given a similar interpretation to heterochromosomes found in other mammals.

MONTGOMERY ('12) who used GUYER's material in part, also reported 2 sex chromosomes in the male. His study led him to the unusual conclusion that at least four classes of sperms are formed (depending on his belief that only one or else both sex chromosomes may undergo the segregation division in either of the meiotic divisions).

Up to this time the various investigators had reported a diploid number of about 24 or less, so that VON WINIWARTE's results published in the same year as MONTGOMERY's created some surprise. That investigator found that the number of chromosomes in the spermatogonia is 47 and that after pseudoreduction there are 24 elements. Since he counted 48 chromosomes in the diploid set of the female he concluded that the male carries an unpaired X. This account bearing all the marks of excellence was deservedly given a great deal of weight, but in spite of this JORDAN ('14b) concluded that the haploid number is only 12 or perhaps slightly higher. WIEMAN ('17) also disagreed with VON WINIWARTE, describing 24 chromosomes in the diploid set which includes an XY pair in the male. It is to be noted here that WIEMAN's X is one of the largest chromosomes and the Y only slightly smaller. Both divide equationally in the primary spermatocyte division and, although direct evidence was not available, probably pass to opposite poles in the second.

It is quite plain at the present time that with the exception of VON WINIWARTE none of the investigators just mentioned had sufficiently well preserved material to enable them to arrive at any

dependable conclusion. All recent work on the chromosomes of the human being makes that fact very evident. In 1921 VON WINIWARter again reported the diploid number of the male as 47 and in this contention was supported by the work of OGUMA and KIHARA ('22, '23). GROSSEr ('21), the excellence of whose preparations is attested not only

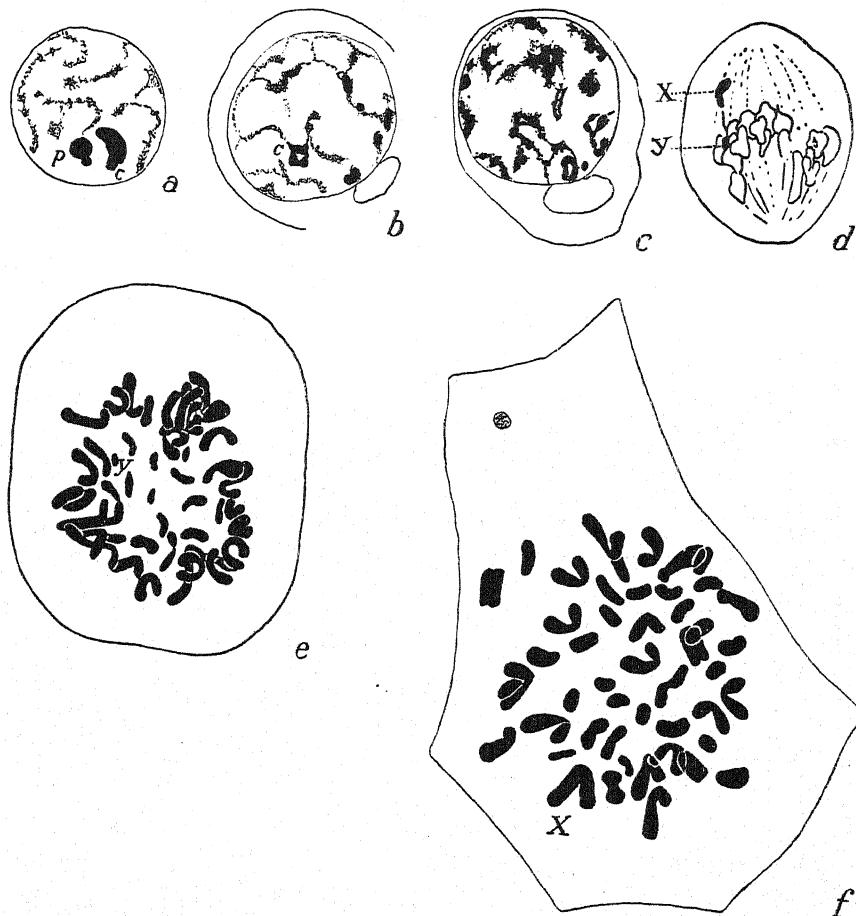


Fig. 42. *Homo sapiens* (PAINTER, '24d)—*a* Late pachytene stage in first spermatocyte, showing chromatin nucleolus (c) and plasmosome (p). *b* Confused stage of first spermatocyte, with chromatin nucleolus decreased in size. *c* Early diakinesis in first spermatocyte. *d* First spermatocyte division. (PAINTER, '23a)—*e* Spermatogonial plate with 48 chromosomes, the smallest chromosome being regarded as the Y. (OGUMA & KIHARA, '23) —*f* Spermatogonial plate with 47 chromosomes, showing a large, unpaired X.

by his drawings but also by some photographs (as reported by PAINTER, '23a) counted in the amnion of different embryos close to 47 or 48 chromosomes. GROSSEr however was loath to believe his own evidence and suggested that this number is due to a precocious splitting of a smaller number of chromosomes. RAPPEPORT's counts ('22) caused him to con-

clude that the diploid number is probably between 40 and 44. CONKLIN ('22) stated that renewed investigation had led GUYER to conclude that 48 is the diploid number (sex not stated) and EVANS (according to BABCOCK and CLAUSEN, '18, pp. 538) came to the same conclusion in his study of spermatogonial cells. It thus seems fairly safe to conclude that the diploid number is 47 or 48.

But the question of sex chromosomes has received no final answer as yet. VON WINIWARTER as well as OGUMA and KIHARA are led to conclude that the male has an unpaired X (fig. 42f). Opposed to this is EVANS' statement that spermatogonia have 48 chromosomes which implies an XY pair, and also all of PAINTER's findings (fig. 42) which confirm that conclusion with strong evidence ('21, '23a, '24d). According to PAINTER, the Y is quite small and easily overlooked. However PAINTER was able to trace the unequal XY pair through the first division and found that these 2 sex chromosomes actually separate at that time and pass undivided to opposite poles. The general behavior of the pair is very much like that of the XY pair as PAINTER has found it in various other mammals and especially in the monkeys. It does not correspond to the chromosomes described by WIEMAN ('17) as the X and Y, and it seems likely that that investigator was concerned with some autosomes.

During the growth stages of meiosis in the male a single chromatin nucleolus is present, and this undergoes a considerable degree of condensation as the metaphase stage is approached. However as early as the later diakinesis phases it becomes difficult to distinguish it from the condensing autosomes and although it appears very likely that it represents the heteropycnosis of the XY pair, the point is not quite certain.

Genetic evidence as published by SCHOFIELD ('21) and pointed out by CASTLE ('21) supports the view that the male has an XY pair of sex chromosomes.

The case may be summed up with the statement that the males certainly represent the heterogametic sex and that their sex chromosomes are either of the XO or the XY type. Beyond that the weight of evidence is not definitely in favor either of the interpretation given by PAINTER, to wit, that there is an XY pair, or that advanced again by de WINIWARTER and OGUMA in 1926, that the male has an unpaired X.

#### VERTEBRATA

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
1. <i>Pisces</i> <i>Gambusia</i> <i>holbrooki</i>	35 or 36 spg.	18	18	—	Sex chromo- somes?	GEISER '24
<i>Lebiasina</i> <i>reticulatus</i>	46 oog.	23 23 ♀	23	—	No cytological evidence of sex chromosomes	WINGE '22b

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Umbra lima</i>	22 spg. 20 $\circ$ soma	11	11	11?	2 heterochromosomes?	FOLEY '26
<b>2. Amphibia</b>						KING '12
<i>Necturus maculosus</i>	—	12	—	—	X attached to an autosome?	
<i>Rana esculenta</i>	25 spg. approx.	13	12 13	—	In need of confirmation	LEVY '15
<i>Rana temporaria</i>	26 spg.	13	13	—	Apparently XY in males	WITSCHI '23
<b>3. Reptilia</b>						
<i>Anguis fragilis</i>	19 macro + 24? micro spg.	10 macro + 12 micro	10 macro 9 macro + ? micro	10 macro 9 macro + ? micro	Probably XO	DALCO '21
<i>Anolis carolinensis</i>	12 macro + 22? micro	5 macro + X <sup>I</sup> X <sup>II</sup> 11 micro	5 macro + X <sup>I</sup> X <sup>II</sup> 11 micro?	5 macro + ? micro	—	PAINTER '19, '21a
	14 macro ♀ soma probably		5 macro + 11 micro?	5 macro + ? micro		
<i>Chrysemis marginata</i>	—	—	—	—	Shows bipartite body in spermatocytes	JORDAN '14
<i>Cistudo carolina</i>	—	—	—	—	Shows bipartite body in spermatocytes	JORDAN '14
<i>Cnemidophorus gularis</i>	—	13 macro + 7 micro	—	—	Probably X <sup>I</sup> X <sup>II</sup> to pole in 1st	PAINTER '21a
<i>Crotaphytus collaris</i>	12 macro + ? micro	6 macro + ? micro	—	—	Probably X <sup>I</sup> X <sup>II</sup>	PAINTER '21a
<i>Holbrookia texana</i>	12 macro + ? micro	5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	—	PAINTER '21a
			5 macro + ? micro	5 macro + ? micro		
<i>Thamnophis butleri</i>	37 spg.	18	18 19	—	Possibly an X <sup>I</sup> X <sup>II</sup> Y	THATCHER '22
<i>Sceloporus undulatus</i> var. <i>consobrinus</i>	12 macro + 18 micro	5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	—	—	PAINTER '21a
			5 macro + ? micro			

Species	Diploid Chromosome Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Sceloporus spinosus</i>	12 macro + 10 micro spg. 14 macro + ? micro ♀ soma	6 macro + 5 micro = 5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	—	—	PAINTER '21a
<i>Uta ornata</i>	12 macro + ? micro	5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	5 macro + X <sup>I</sup> X <sup>II</sup> + ? micro	—	—	PAINTER '23a
4. Aves						
<i>Columba livia</i> dom.	61 & 62 embryos 62 spg.	31	31	—	ZO in female	OGUMA '27
<i>Gallus gallus</i> dom.	32—40 spg. and embryo	18—20	—	—	ZO or WZ in female	AKKERINGA '27 GUYER '16 BORING '23 HANCE '24, '26 SHIWAGO '24
<i>Numidia melagris</i> dom.	17 spg.	9	5 (= 9) 4 (= 8)	5	Thought XO in male; probably not correct	GUYER '09a
5. Mammalia						
A. Marsupialia						
<i>Dasypurus maculatus</i>	14 spg.	—	—	—	—	GREENWOOD '23
<i>Didelphis virginiana</i>	22 spg. 22 ♀ soma	10 + XY 10 + Y	10 + X 10 + Y	10 + X 10 + Y	—	HARTMANN '19 PAINTER '22a, '24a JORDAN '11
<i>Macropus ualabatus</i>	11 or 12 spg. 10 (= 12) ♀ soma	5 + XY 5 + Y	5 + X 5 + Y	5 + X 5 + Y	XY attached to autosome	AGAR '23
<i>Petauroides volans</i>	21 spg.	—	—	—	Presence of XY in male not certain	AGAR '23
<i>Phascolarctus cinereus</i>	16 spg. 16 ♀ soma	7 + X + Y 7 + Y	7 + X 7 + Y	7 + X 7 + Y	—	GREENWOOD '23

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<i>Phascolomys mitchelli</i>	—	6 + XY	—	—	X and Y to opposite poles in 1st	ALTMANN & ELLERY '25
<i>Potorous tridactyla</i>	12 spg. 12♀ soma	5 + XY 5 + Y	5 + X 5 + Y	—	—	ALTMANN & ELLERY '25
<i>Pseudochirus peregrinus</i>	20 spg. 20♀ soma	9 + XY 9 + Y	9 + X 9 + Y	—	2nd division equational for sex chromosomes	ALTMANN & ELLERY '25
<i>Sarcophilus ursinus</i>	14 spg. 14♀ soma	—	—	—	XY to poles in 1st	GREENWOOD '23
<i>Trichosurus vulpecula</i>	20 spg. 20♀ soma	9 + XY 9 + Y	9 + X 9 + Y	—	—	ALTMANN & ELLERY '25
B. Edentata <i>Tatu novemcinctum</i>	60 amnion	—	—	—	Probably XY in male	PAINTER '25 a, '25 b NEWMAN '12 NEWMAN & PATTERSON '10
C. Ungulata <i>Bos taurus</i>	38 oog. 37 spg.	—	—	—	XO in male? Counts not final	WODSEDALEK '20 MASUI '19 b
<i>Equus caballus</i>	60 spg.	30	—	—	XO or XY in male Counts not final	WODSEDALEK '14, '16 MASUI '19 a PAINTER '24 c
<i>Ovis aries</i>	—	—	—	—	XO in male? Not certain	JORDAN '14 b
<i>Sus scrofa</i>	40 spg.	20	—	—	WODSEDALEK reported unpaired $X^I X^{II}$ for the male. Questionable	WODSEDALEK '13 a, '13 b JORDAN '14 b HANCE '17 b
D. Carnivora <i>Canis familiaris</i>	50 at least amnion	—	—	—	Unpaired $X^I X^{II}$ (MALONE) or XY (PAINTER)	MALONE '18 PAINTER '25 b
<i>Felis domestica</i>	50 approx. embryo	—	—	—	XO in male?	V. WINIWARTER & SAIN-MONT '09 HANCE '17 a GUTHHERZ '25 V. WINIWARTER '14

Species	Diploid Chromo- some Number	Meiotic Chromosomes (male, unless otherwise stated)			Remarks	Reference
		1st cyte	2nd cyte	tid		
<b>E. Rodentia</b>						
<i>Mus musculus</i>	40 spg.	20	20	—	Probably XY in male	COX '26 YOCUM '17 GUTHERZ '22 MASUI '23 JORDAN '14 b
<i>Mus rutilus</i>	37 spg. 37♂ soma	18 + X	18 18 + X	—	In need of confirmation	ALLEN '18 LONG & MARK '11
<i>Mus sylvaticus</i>	—	—	—	—	1 hetero- chromosome?	FEDERLEY '19
<i>Lepus cuniculus</i>	44? amnion	—	—	—	Probably XY in male but MASUI thinks XO	BACHHUBER '16 MASUI '23 PAINTER '25 a, '25 b
<i>Cavia cobaya</i>	56 spg. probably	28	—	—	XY in male	STEVENS '11 b, '11 c HARMAN & ROOT '26
<b>F. Cheiro- ptera</b>						
<i>Vesperugo?</i>	40? spg.	—	—	—	XO or XY in male	JORDAN '12 HANCE '17 a
<i>Nyctonomus mexicana</i>	48 amnion	—	—	—	XY in male	PAINTER '25 a, '25 b
<b>G. Primates</b>						
<i>Brown Cebus</i>	54 spg.	26 + XY	26 + X 26 + Y	—	—	PAINTER '22 b, '23 b, '24 c
<i>Homo sapiens</i>	48 spg. 48 em- bryo	28 + XY	23 + X 23 + Y	—	V. WINIWARTER and OGUMA and KIHARA think male = XO	V. WINIWARTER & OGUMA '26 V. WINIWARTER '12, '21 PAINTER '21 b, '23 a, '24 d OGUMA & KIHARA '22, '23
<i>Rhesus macacus</i>	48 spg. 48♂ soma 48♀ soma	28 + XY	23 + X 23 + Y	—	—	PAINTER '22 b, '23 b, '24 c

## PLANTS

Although experimental evidence established many years ago that in most plants the male represents the heterogametic sex (CORRENS, '07; DOUIN, '09; SHULL, '10, '11; BAUR, '12), no definite demonstration of sex chromosomes was made until 1917. It is true that CARDIFF ('06) described a heterochromosome in *Salomonia biflora*, but that plant is hermaphroditic or monoecious and even if CARDIFF's observations are perfectly correct the chromosome in question is probably not a sex chromosome. Again, in 1911 NAWASCHIN described in *Tradescantia* a chromatin nucleolus and pointed out its resemblance to the sex chromosomes that had been described in many animals. But here too there now seems little doubt that he was not dealing with a sex chromosome.

DARLING's reports of a "difference in the chromatin substance in half the nuclei" of *Acer* has been shown to be erroneous by both MOTTIER ('14) and TAYLOR ('20). Negative evidence on the other hand was reported by STRASBURGER ('09, '10) and SYKES ('09), whose attempts to find sex chromosomes in a number of plants proved unsuccessful.

Thus ALLEN ('17, '19) was the first to show that sex chromosomes are certainly present in some plants. He found that in *Sphaerocarpus donnellii* the female gametophyte carries 7 autosomes and a large X chromosome, while in the male gametophyte there are seven autosomes and a small Y. The diploid group of the sporophyte showed that there also the large X can be recognized, but it was not possible to distinguish the Y from the autosomes. A corroboration of these findings in *Sphaerocarpus texanus* was published by SCHACKE ('19). Finally, LORBEER ('27) has confirmed these accounts and given additional evidence.

More recently sex chromosomes have been reported by various investigators in a large number of plants (fig. 43). In the phanerogams, such chromosomes were first described in *Elodea* by SANTOS ('23, '24). He reported in the male sporophyte about 48 chromosomes, including one unequal pair. No such unequal pair could ever be found in the female sporophyte. Although SANTOS felt justified in assuming that the unequal pair represents an X and Y, he did not commit himself in identifying either member of the pair as the X or the Y.

Rather more unusual conditions were described by KIHARA and ONO ('23a, '23b) in *Rumex acetosa*. In the diploid cells of the male they reported 15, while in the female they found only 14 chromosomes. In the heterotypic division of the pollen mother cells are found 6 auto-some bivalents and a sex chromosome group of 3 chromosomes. The largest of the latter goes to one pole while the other two chromosomes go to the opposite pole. Since the bivalents divide normally, there are formed two daughter groups with 7 and 8 chromosomes respectively. The evidence therefore seems complete that here there is one of the very rare cases of a compound Y. SINOTO ('24) who reinvestigated this plant, reported that KIHARA's and ONO's general conclusions are correct, but thought that some of his own figures suggested the possibility that the large and one of the smaller sex chromosomes may on rare occasions go to the same pole. Finally, MEURMAN ('25) has confirmed KIHARA's and ONO's findings in *Rumex thrysiflorus*, but indicated that in *Rumex*

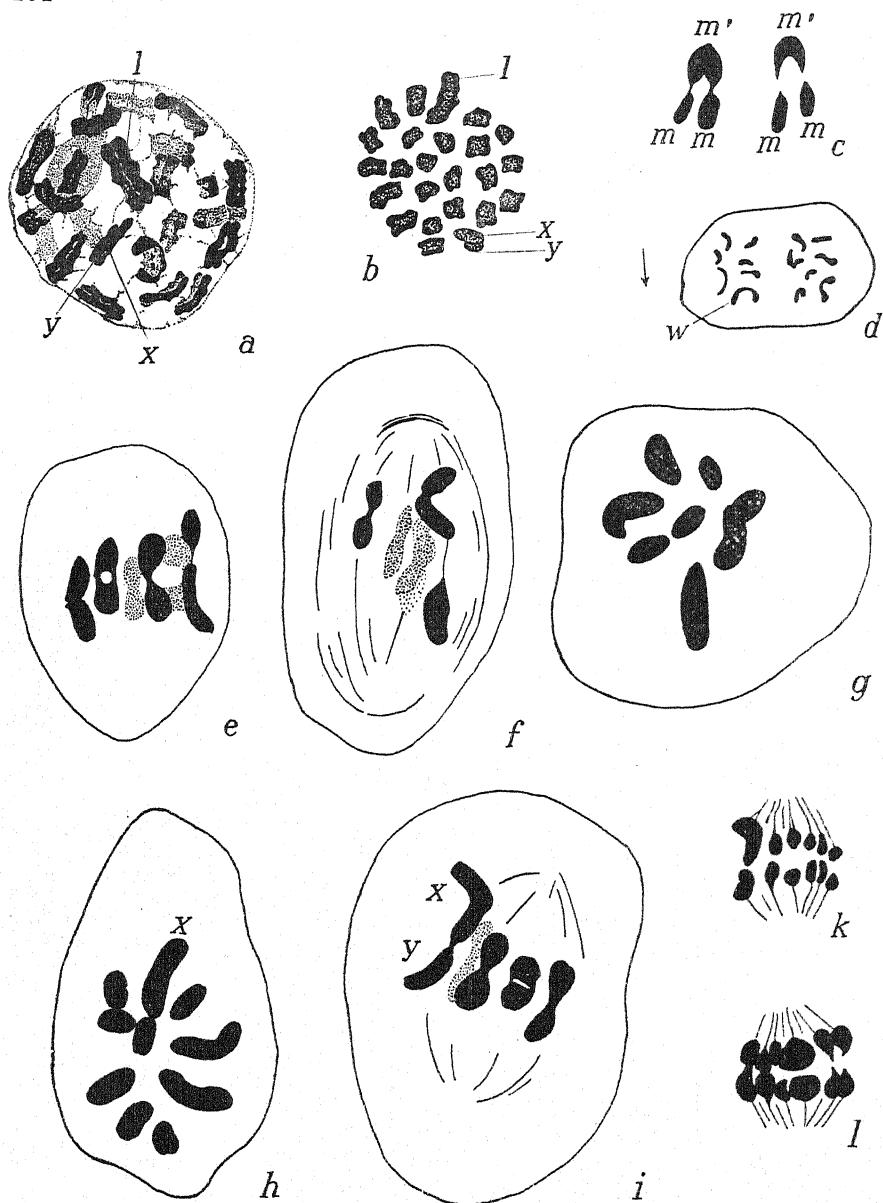


Fig. 43. Plants. (BĚLAŘ, '24a)—*Elodea gigantea* (after SANTOS). *a* Diakinesis and *b* Metaphase of first meiotic division in male (*l* = large autosomal pair). *Rumex acetosa* (after KIHARA & ONO). *c* Sex chromosomes from metaphase of first meiotic division in male.  $m' = X$ ,  $mm = Y$ . *d* Two metaphases of equational meiotic division, showing 7 and 8 chromosomes respectively. *Humulus lupulus* (after WINGE). *e* Side view of first meiotic division in male, showing unequal XY pair. *Humulus japonicus* (after WINGE). *f* Same as *e*. *Vallisneria spiralis* (after WINGE). *g* & *h* Metaphases of equational meiotic division in male, showing 8 and 8 plus X respectively. *Melandrium album*. *i* (after WINGE) Side view of first meiotic division in male, showing unequal XY pair. *k* & *l* (after BLACKBURN) First meiotic division in male and female respectively, only the former showing unequal chromosome pair.

*acetosella* a  $X^1X^2Y$  condition may obtain. His proof for the last named case is however not complete. Evidence for such a compound X has also been reported for two species of *Pellia* by LORBEER ('27).

Little more need be said in regard to several other plants in which sex chromosomes have been found. In some cases, as for instance *Melandrium*, some difference of opinion exists as to whether the larger or the smaller of the sex chromosomes in the male represents the X. WINGE ('23 b), without investigating the female cells assumed the larger of the unequal pair to represent the X, but Miss BLACKBURN ('23, '24) on the basis of an examination of both male and female cells came to the conclusion that it is the smaller chromosome in the male that is to be identified as the X. HEITZ ('25) and MEURMAN ('25 b) are inclined however to agree with WINGE. Mention should be made also of the fact that BĚLÁŘ ('25) was able to give a cytological demonstration of a conclusion that had already been reached on genetic evidence,—that hermaphroditic plants of *Melandrium* are basically male and carry an XY pair just like true males. The difference in size between the X and Y of *Melandrium* is so great that it must ever remain a puzzle how so astute an observer as STRASBURGER could have overlooked these chromosomes when he investigated the plant for sex chromosomes.

Of considerable interest, especially in connection with the origin of polyploid forms, is the discovery made by HARRISON ('26), that in several polyploid species of Salicaceae only one pair of sex chromosomes is present.

A more intense study of the growth stages preparatory to meiosis seems called for in future investigations of sex chromosomes in plants. The danger of identifying every heterochromosome as a sex chromosome is just as great in plants as it is in animals and it is to be hoped that this tendency will be checked by a study of the homogametic individuals.

Species	Diploid Chromo- some Number	Meiotic Chromosomes			Remarks	Reference
		Dia- kinesis	Results of 1st division (Hetero- type)	Results of 2nd division (Homo- type)		
<i>Cannabis sativa</i> („To-diego“ race)	20 ♂ 20 ♀	9 + XY	9 + X 9 + Y	9 + X 9 + Y	Mc PHEE was unable to find sex chromosomes	HIRATA '24 Mc PHEE '24
<i>Dioscorea sinuata</i>	35 ♂ approx.	17 + X?	17 + X? 17 ?	17 + X? 17 ?	Not certain of numbers or sex chromosomes	MEURMAN '25 b JORGENSEN '27
<i>Elodea canadense</i>	48 ♂ 48 ♀	23 + XY	23 + X 23 + Y	23 + X 23 + Y	—	SANTOS '23, '24
<i>Elodea gigantea</i>	48 ♂ 48 ♀	23 + XY	23 + X 23 + Y	23 + X 23 + Y	—	SANTOS '23, '24

Species	Diploid Chromosome Number	Meiotic Chromosomes			Remarks	Reference
		Diakinesis	Results of 1st division (Heterotype)	Results of 2nd division (Homotype)		
<i>Humulus japonicus</i>	20 ♂ 20 ♀	9 + XY 9 + Y	9 + X 9 + Y	9 + X 9 + Y	—	WINGE '23
<i>Humulus lupulus</i>	20 ♂ 20 ♀	9 + XY 9 + Y	9 + X 9 + Y	9 + X 9 + Y	—	WINGE '23
<i>Melandrium (Lychnis) album</i>	24 ♂ 24 ♀	11 + XY 11 + Y	11 + X 11 + Y	11 + X 11 + Y	—	HEITZ '25 BĚLÁŘ '25 BLACKBURN '23, '24 WINGE '23 MEURMAN '25 b
<i>Melandrium (Lychnis) rubrum</i>	24 ♂ 24 ♀	11 + XY 11 + Y	11 + X 11 + Y	11 + X 11 + Y	—	MEURMAN '25 b BLACKBURN '24
<i>Pellia fabroniana</i>	16	7 + X <sup>I</sup> + X <sup>II</sup> or 7 + X <sup>I</sup> X <sup>II</sup>	7 7 + X <sup>I</sup> + X <sup>II</sup>	—	LORBEER's figures not conclusive on behavior of X <sup>I</sup> and X <sup>II</sup> prior to first	LORBEER '27
<i>Pellia neesiana</i>	16	7 + X <sup>I</sup> + X <sup>II</sup> or 7 + X <sup>I</sup> X <sup>II</sup>	7 7 + X <sup>I</sup> + X <sup>II</sup>	—	LORBEER's figures not conclusive on behavior of X <sup>I</sup> and X <sup>II</sup> prior to first	LORBEER '27
<i>Populus balsamifera</i>	38 ♂ 38 ♀	19	18 + X probably 18 + Y probably	—	BLACKBURN & HARRISON give diploid number as 76	MEURMAN '25 b BLACKBURN & HARRISON '24
<i>Populus simoni</i>	38 ♂ 38 ♀	—	—	—	Extent of pairing is variable. Two heterochromosomes present	MEURMAN '25 b
<i>Populus tremula</i>	38 ♂ 38 ♀	19	19	—	Possibly sex chromosomes present	BLACKBURN & HARRISON '22, '24
<i>Populus trichocarpa</i>	—	19	18 + X probably 18 + Y probably	—	—	MEURMAN '25 b
<i>Riccia bischoffii</i>	16	8	8	—	Probably an XY	LORBEER '27
<i>Riella helicophylla</i>	14 + X + Y	7 + XY	7 + X 7 + Y	—	—	LORBEER '27

Species	Diploid Chromosome Number	Meiotic Chromosomes			Remarks	Reference
		Dia-kinesis	Results of 1st division (Hetero-type)	Results of 2nd division (Homo-type)		
<i>Rumex acetosa</i>	15 ♂ 14 ♀	6 + XY <sup>I</sup> Y <sup>II</sup>	6 + X 6 + Y <sup>I</sup> + Y <sup>II</sup>	6 + X 6 + Y <sup>I</sup> + Y <sup>II</sup>	—	KHARA & ONO '23 a, '23 b SINOTO '24
<i>Rumex acetosella</i>	—	20	20 ? 21 ?	—	Possibly X <sup>I</sup> X <sup>II</sup> Y in male	MEURMAN '25 b
<i>Rumex thrysiflorus</i>	—	6 + XY <sup>I</sup> Y <sup>II</sup>	6 + X 6 + Y <sup>I</sup> + Y <sup>II</sup>	—	—	MEURMAN '25 b
<i>Salix aurita</i>	76 ♂ 76 ♀	38	38	—	Possibly XY in male. Frequent irregularities in 2nd division	BLACKBURN & HARRISON '24 HARRISON '26
<i>Salix cinerea</i>	76 ♂ probably 76 ♀ probably	38	38	—	Possibly XY in male	BLACKBURN & HARRISON '24 HARRISON '26
<i>Salix lucida</i>	70 + ♂	38	—	—	Possibly XY in male	HARRISON '26
<i>Salix viminalis</i>	38 ♂ 38 ♀	19 19 ♀	19	—	Possibly sex chromosomes present	BLACKBURN & HARRISON '24
<i>Sphaero-carpus donnellii</i>	16	—	7 + X 7 + Y	7 + X 7 + Y	—	ALLEN '17, '19 LORBEER '27
<i>Sphaero-carpus terrestris</i>	14 + X + Y	7 + XY	7 + X 7 + Y	—	—	LORBEER '27
<i>Sphaero-carpus texanus</i>	16	—	7 + X 7 + Y	7 + X 7 + Y	—	SCHACKE '19 LORBEER '27
<i>Urtica dioica</i>	—	24 probably	—	—	Two hetero- chromosomes in male	MEURMAN '25 b
<i>Valeriana dioica</i>	—	8	8	—	Possibly XY in male	MEURMAN '25 b
<i>Vallisineria spiralis</i>	—	—	8 + X ? 8	—	JORGENSEN found no sex chromosomes	WINGE '23 JORGENSEN '27

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